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EMBRYONIC DEVELOPMENT OF THE HUMAN FOOT WITH SPECIAL REFERENCE TO CONGENITAL ANOMALIES

by

© PATRICIA ROSALIND McKEE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Supervisor

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Date...Oct. 9, 1985.....

Abstract

The purpose of this study was to examine the postures and musculoskeletal structures of the human foot during the final stages of embryonic development. Six serially sectioned embryos of stages 20 to 23 (21.7mm to 34.0mm crown rump length) were selected for study. Three-dimensional reconstruction involving wax-plate and transparency models was used to recreate the embryonic foot of four of the specimens and this was supplemented by microscopic examination of the serial sections. The other two embryos were studied solely by microscopic examination. At least one model from each of the three planes of section was produced to ensure a clear understanding of the spatial arrangement of the internal structures. For each embryo, the relationships of the musculoskeletal elements were determined, paying particular attention to the attachment sites of the muscles. These observations were compared with findings from a dissected adult lower limb, as representative of the end point of the developmental continuum.

In contrast with much of the previous literature, the skeletal relationships of the embryos were found to be similar to the adult condition; the calcaneus was situated below the talus; the fibula projected further distally than the tibia; and there was no evidence that the tip of the fibular malleolus was in contact with the calcaneus. However, numerous differences in the posture and

musculoskeletal structures between the embryonic and adult foot were identified. These differences centred on the sites of muscle attachment and the apparent tendon-axis relationships. For example, the relatively later distal attachment of the peroneal tendons suggested that until the final stages of embryonic development, the muscles that are acting to adduct and invert the forefoot (i.e. tibialis anterior and posterior) would be largely unopposed. This was thought to account in part for the inversion adduction of the embryonic foot. Also identified was the relatively late distal attachment of the tendons terminating in the toes and the delayed proximal attachment of abductor hallucis and flexor digitorum brevis. Although the factors involved in the postural changes during ontogeny were not investigated directly, differential growth of the skeletal elements as well as changing muscle function were identified as two possibilities.

The striking similarities between the postures and pathoanatomy of talipes equinovarus (clubfoot) and the features of the embryonic foot lend support to the contention that this congenital anomaly is characterized by the persistence of certain embryonic features. Furthermore, other less severe congenital anomalies, such as metatarsus adductus or calcaneal varus, seem to occur when only one or two embryonic features have been retained.

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Dedication

To Ron, Sarah and Alice whose understanding, support and encouragement helped me to achieve this goal.

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I. INTRODUCTION

The embryonic development of the human foot has been studied for more than a century by many workers. Whereas the histogenesis of the musculoskeletal structures has been documented extensively, there is a general lack of information pertaining to the relationships and attachments of muscles in the embryonic foot. In addition, there are conflicting accounts concerning the relationships of the skeletal elements. Furthermore, there appear to have been no studies that have considered how muscle action could alter the postures of the prenatal foot.

Several workers have reported the striking similarity between the postures of the embryonic foot and talipes equinovarus (congenital clubfoot) and have concluded that "arrested development" is the primary cause of clubfoot (Bohm, 1929, Martinez-Cuadrado and Gonzalez-Santander, 1967; Victoria-Diaz and Victoria-Diaz, 1984). Numerous other theories have also been proposed and investigated, but as yet no primary etiological factor has been identified. One of the principal contributing factors is the disparity of opinions as to which of the skeletal and muscle abnormalities represent primary defects in contrast to secondary adaptive changes. A thorough and convincing investigation of the etiological theory of "arrested development" requires a comprehensive understanding of the musculoskeletal development in the embryonic foot. Unfortunately, this process has not been fully documented as

yet. Furthermore, until the mechanisms controlling the postural changes in the embryonic foot are fully understood, any theories that implicate arrested development as the primary cause of clubfoot, can be neither confirmed nor disproved.

The present study shall examine the size, shape and relationships of the musculoskeletal elements in the foot of serially sectioned human embryos with the following objectives:

1. to identify the factors that may be responsible for the postural features of the embryonic foot
2. to compare the characteristics of the musculoskeletal elements in the embryonic foot with the pathoanatomical features of various congenital foot anomalies as reported in the literature, investigating the etiological theory of "arrested development".

II. REVIEW OF LITERATURE

A. THE PRENATAL DEVELOPMENT OF THE HUMAN FOOT

Studies of the prenatal development of the human foot date from 1880. Generally speaking, these investigations fall into one of three categories. Firstly, there are those workers who have studied this topic simply to understand better the early development of the foot. The majority of the literature falls into this category (Leboucq, 1882, cited in Jones, 1949; Schomburg, 1900, cited in Bohm, 1929; Bardeen and Lewis, 1901; Bardeen, 1905; O'Rahilly, 1953, 1957 and 1973; O'Rahilly, Gardner and Gray, 1956; O'Rahilly, Gray and Gardner, 1957; Gardner, Gray and O'Rahilly, 1959; Huson, 1969; Blass, 1974; O'Rahilly and Gardner, 1975). A second group of investigators, using Hæckel's recapitulation theory (Gould, 1977) as a guiding principal, have studied the ontogeny of the human foot as a basis for interpreting its phylogeny (Straus, 1927; Keith, 1929: Schultz, 1930; Cihak, 1972; Crelin, 1983). Thirdly, there are those workers whose primary objective was to investigate the theory of "arrested embryonic development" as the primary cause of congenital clubfoot (Bohm, 1929; Martinez-Cuadrado and Gonzalez-Santander, 1967; Victoria-Diaz and Victoria-Diaz, 1984).

Aging of the Embryos

The initial problem in any embryonic study is to determine the age of the specimens. Unfortunately, the method varies among workers so that it is often difficult to compare the findings reported in the various studies. The majority of the investigators who have studied the prenatal development of the foot have used the crown-rump length (CRL) as an indication of the relative maturity of the embryo (Bardeen and Lewis, 1901; Bardeen, 1905; Bohm, 1929; Jones, 1949; Olivier, 1962; Martinez-Cuadrado and Gonzalez-Santander, 1967; Cihak, 1972; Victoria-Diaz and Victoria-Diaz, 1984). Some workers have then estimated the approximate age from the CRL based on various formulae (Arey, 1940; Hamilton, Boyd and Mossman, 1978). There are two problems associated with this documentation. Firstly, the workers have not always defined whether the maturity is expressed in terms of postmenstrual or postovulatory age. Secondly, there is considerable variation in the degree of flexion between embryos of similar maturity which makes the measurement of CRL unreliable. Therefore CRL should not be regarded as a precise indication of the gestational age (Bagnall, Jones and Harris, 1975).

An alternate method of aging embryos was developed by Streeter (1948 and 1951). He surveyed the extensive Carnegie collection of embryonic material and determined that growth and differentiation of various body tissues and organs conforms to a rigid seniority schedule. Based on his

observations, he divided the embryonic period into 23 developmental horizons or stages and defined each stage in terms of the progressive development of specific key structures (the cornea, optic nerve, cochlea, hypophysis, vomeronasal organ, submandibular gland, kidney, cartilage and bone). He then "staged" each of the Carnegie embryos by assigning each to a developmental horizon and estimated the postovulatory ages by comparing each specimen with macaque embryos of known ovulation age. Although Streeter's (1948 and 1951) method of aging embryos appears to be more reliable than CRL as an indication of relative maturity, it has only been used in a few studies which have had access to the Carnegie collection (O'Rahilly, 1953, 1957, 1973; O'Rahilly *et al.*, 1956, 1957; Gardner *et al.*, 1959).

In 1957, O'Rahilly *et al.* re-examined the Carnegie collection of staged embryos and, for each of the stages 15 to 23, they defined more precise criteria related to the chondrification in the foot. These criteria permit other investigators to examine serially sectioned embryos and determine their stage of development based entirely on the chondrification in the foot.

Development of the External Form

The most comprehensive reference concerning development of the external form of the lower limb during the embryonic period is the series of photographs compiled by Streeter (1948 and 1951) in which a large number of staged embryos

from the Carnegie collection were presented in order of their increasing maturity. In addition, numerous workers have described the changing external appearance of the limb (Bardeen and Lewis, 1901; Bohm, 1929; Blechschmidt, 1969; O'Rahilly, 1973; O'Rahilly and Gardner, 1975). According to these accounts, development of the lower limbs begins during the fifth postmentrual week, Streeter's stage 13, when the lower limb bud is first seen as an amorphous projection from the lateral wall of the body. By stage 16, the thigh, leg and foot regions can be discerned. Then the foot region becomes flattened into what is called a paddle-shaped foot plate. The formation of the toes begins during stage 19 when five radiating columns of denser material, representing the toe rays, are seen in the foot plate. In stage 20, the clefts between the toes begin to form by selective necrotic changes of the ectoderm and mesoderm between the toe rays. By the end of the second month (stage 23), the toes are well developed.

The growth and maturation of the embryonic limb has been described by some workers as proceeding in a proximodistal fashion, controlled in part by the transitory apical ectodermal ridge (O'Rahilly *et al.*, 1956; Carlson, 1981). However, it is apparent that the proximodistal maturation occurs only in general terms and there are several exceptions to this trend. For example, several workers have observed that the the first elements to chondrify in the foot are the metatarsals (Bardeen, 1905;

Bohm, 1927; Gardner *et al.*, 1959).

Postural Changes

During ontogenetic development, there are pronounced changes of position which are due in part to medial rotation of the lower limbs. These postural changes are clearly apparent from Streeter's (1948 and 1951) photographic series of staged embryos and have been described by numerous investigators (Schomburg, 1900; Bardeen, 1905; Bohm, 1929; O'Rahilly and Gardner, 1975; Victoria-Diaz and Victoria-Diaz, 1984). According to these reports, when the foot plate first differentiates, at about six postovulatory weeks, the future sole faces cranially and toward the umbilical cord while the future dorsum of the foot is directed laterally and caudally. During the next two weeks, the limbs grow progressively longer and their original lateral orientation is gradually changed to a more anterior position. At the same time, the limbs rotate medially such that the soles come to face each other. By the end of the embryonic period, the posture of the foot is one of marked plantar flexion at the ankle joint, adduction of the foot toward the tibia and inversion (or supination). The tibial border of the limb is directed cranially with the extensor (future anterior) surface of the limb facing laterally and the flexor (future posterior) surface, including the sole, directed medially. O'Rahilly (1973) described it as the "praying feet" posture.

The embryonic position of the foot is markedly different from the anatomical position of the adult lower limb. The medial rotation that begins during the embryonic period, continues during the fetal period and into postnatal life to rotate the tibial border downwards and the fibular border upwards until the sole of the foot is directed toward the ground. Although the factors influencing these changes have not been clearly defined (O'Rahilly and Gardner, 1975), some workers, including Bohm (1929) and Cailliet (1983), have implicated inadequate medial rotation of the lower limb, due to arrested embryonic development, as the primary cause of congenital clubfoot. Similarly, Victoria-Diaz and Victoria-Diaz (1984), postulated that a temporary arrest of growth of the skeletal elements on the tibial side of the limb causes the foot to remain in its embryonic position, resulting in the clubfoot deformity.

Skeletal Development

The differentiation of the internal structures of the lower limb has been studied from serial sections, using light microscopy. The majority of these studies focus on the histogenesis of the various tissues, with particular emphasis on the chondrification of the skeletal elements and joint formation (Schomburg, 1900; Bardeen and Lewis, 1901; Bardeen, 1905; Bohm, 1929; Senior, 1929; Haines, 1947; Streeter, 1949; O'Rahilly *et al.*, 1957; Gardner *et al.*, 1957; Drachman, 1969; Cihak, 1972; O'Rahilly and Gardner,

1975). The most extensive review of skeletal development in the prenatal foot was done by Gardner *et al.* (1959) who examined 184 serially sectioned embryos and fetuses and consulted 104 references. Their paper focused on the timing and description of chondrification, ossification and joint formation. Cihak (1972), who studied 56 histological series from the feet of embryos and fetuses from 15 to 40mm CRL, observed that the ontogenetic changes occurring in the human skeleton were strikingly similar to the process of changes found in the course of phylogenesis. He concluded that in the course of ontogenesis, the sequence of form changes is the same as in the phylogenetic past due to developmental recapitulation.

Many workers have reported changes in the proportionate sizes of the skeletal elements during the ontogenetic process, in particular a relative increase in the length of the tarsus and the hallux and a relative decrease in the length of the outer four rays (Straus, 1927; Keith, 1929; Schultz, 1930). These workers also reported that the proportionate sizes of the skeletal elements in the human embryo are similar to those seen in adult apes and, like Cihak (1972), concluded that the ontogenetic changes represent a recapitulation of phylogenetic changes.

Deviations of skeletal development that give rise to accessory ossicles, multipartitions and tarsal coalitions in the foot have been described by O'Rahilly (1957), Gardner *et al.* (1959) and Cihak (1972).

Relationships of the Skeletal Elements

Although there is extensive documentation concerning the chondrification and joint formation in the embryonic foot, the literature lacks a comprehensive study of the orientation and relationships of the developing skeletal elements. Furthermore, the reported findings often conflict which can be attributed in part to varying methods of inquiry. A small number of investigators have studied this aspect of development using three-dimensional reconstructions (Schomburg, 1900, cited in Bohm, 1929; Bardeen, 1905; Straus, 1927; Bohm, 1929; Olivier, 1969; Martinez-Cuadrado and Gonzalez-Santander, 1969; Huson, 1969). Other investigators have interpreted the relationships of the skeletal elements without the aid of reconstructions, based solely upon serial sections (Leboucq, 1882, cited in Jones, 1949; Jones, 1949; Blass, 1974; Victoria-Diaz and Victoria-Diaz, 1984). Verbout (1985) stressed that reliable interpretation requires that each stage of development be analyzed from specimens in each of the three planes of section. He also recommended a series of closely graded stages. Unfortunately, none of the forementioned studies met all of these requirements.

Many workers have reported that initially the tibia extends further than the fibula (Bardeen, 1905; Straus, 1927; Jones, 1949; Victoria-Diaz and Victoria-Diaz, 1984). Apparently, Schomburg (1900) stands alone in stating that from the outset, the fibula extends further distally than

the tibia.

Several investigators have also interpreted the embryonic relationships of the talus, calcaneus, tibia and fibula to be strikingly different from the adult situation. For example, Schomburg (1900) was the first to report that initially the fibula rests upon the calcaneus and the tibia articulates with the talus. It has also been reported that initially, the calcaneus lies next to the talus (Bardeen, 1905; Bohm, 1929; Olivier, 1962; Martinez-Cuadrado and Gonzalez-Santander, 1967; Victoria-Diaz and Victoria-Diaz, 1984). From a developmental and functional viewpoint, this talocalcaneal relationship is of primary importance.

The most comprehensive account of the changing talocalcaneal relationship was documented by Bohm (1929), based on the observations from four wax-plate reconstructions. In the 18mm embryo, Bohm (1929) described the calcaneus as lying next to the talus on its lateral side, but in the 23mm embryo (end of the second month), he reported that it had shifted down (plantarwards) below the talus. In the 35mm embryo (middle of the third month), Bohm (1929) observed that the dorsal surface of the calcaneus was tilted laterally and the plantar surface was tilted medially due to marked supination of this bone in relation to the talus. Consequently, the posture of the foot as a whole is one of marked supination. In the 57mm embryo (end of the third month), Bohm (1929) noted that the calcaneus was appreciably less supinated than before. The foot was now in

a position of mid-supination such that a line through the metatarsal heads formed an angle of about 45° with the theoretical horizontal weight-bearing plane of the foot.

Victoria-Diaz and Victoria-Diaz (1984) speculated on the mechanisms influencing the talocalcaneal relation. They proposed that a growth spurt of the distal end of the fibula, occurring from 20 to 30mm CRL, pushes the calcaneus beneath the talus and into supination and that supination of the calcaneus is subsequently reduced during the early fetal period by a tibial growth spurt. Unfortunately, it is apparent from the description of their methodology, that each developmental stage that they examined was not represented by specimens in each of the three sectional planes. In particular, many of the specimens up to 26mm CRL were sectioned obliquely and none of these smaller embryos were sectioned in the coronal plane. Therefore, they may have misinterpreted the skeletal relationships in the hindfoot.

Straus (1927) devised a method of determining the "torsion of the calcaneus which serves as an index for the supination of the foot". He measured the angle between the long axis of the tibia and the long axis of the calcaneal tuberosity and reported that the torsion of the calcaneus was reduced from about 37° in the three month fetus to about 3.5° in the adult. Unfortunately, it is not clear from his description whether the reduction of the angle can be attributed to eversion of the calcaneus, remodelling of the

calcaneal tuberosity or a combination of both.

Straus (1927) also documented certain changes in the talus. He measured the angle between the long axis of the body and neck of the talus and reported that this angle reduced from about 33 degrees in the four month old fetus to approximately 22 degrees in the adult. He concluded that the medial inclination of the talar neck exhibits a very pronounced ontogenetic decrease. Bohm (1929) reported medial inclination of both the talus and the calcaneus which he thought accounted for the adducted posture of the embryonic foot.

According to Straus (1927), during the ontogeny of the human foot, the long axis of the articular surface of the talar head undergoes a rotation due to torsion of the talar neck. He reported that the angle between this long axis and the trochlear surface was less than 20 degrees in the midterm fetus and about 40 degrees in the adult. Jones (1949) interpreted that the torsion of the talar neck occurs as the tibial margin of the forefoot is rotated downwards (everted) during fetal and postnatal life to direct the sole toward the ground. He added that the changing posture of the forefoot of the fetus coincides with the tendon of peroneus longus gaining its insertion to the first cuneiform, in addition to its first metatarsal attachment.

Divergence of the first metatarsal from the second metatarsal during the embryonic period has been reported by Leboucq, 1882, Straus (1927), Bohm (1929), Keith (1929),

Morton (1942), and Cihak (1972). This embryonic characteristic has been attributed to the extreme angle of the facet of the first cuneiform for the first metatarsal. Whereas adduction of the first metatarsal (metatarsus primus varus) is characteristic of the embryonic foot, metatarsus adductus is characteristic of the early fetal period (Bohm, 1929; Keith, 1929). Keith (1929) attributed this postural change to the movement of the outer four metatarsal heads towards the already adducted, static first metatarsal head.

Although postural changes during ontogenetic development as well as changes in the relationships of the skeletal elements have been described by numerous writers, the mechanisms involved in these changes have received very little attention. As previously stated, Victoria-Diaz and Victoria-Diaz (1984) proposed that postural changes during the early prenatal life are due to differential growth of the skeletal elements. There appear to have been no studies that have considered how muscle action could alter the postures of the prenatal foot, although Stewart (1951), Turco (1981) and Jahss (1982) have reported that anomalous tendon insertions may account for the postures seen in the clubfoot. Until the mechanisms controlling the postural changes in the embryonic foot are understood, any theories that implicate arrested development and the concommitant persistence of the embryonic posture as the primary cause of clubfoot, can be neither confirmed or disproved.

Muscular Development

Development of the lower limb musculature has been studied in only very general terms. Until the mid-1970's, it was thought that the myogenic cells of the embryonic limbs originated from the limb mesenchyme (e.g. Bardeen and Lewis, 1901). However, Christ *et al.* (1977) and Chevalier *et al.* (1977) demonstrated that in chick-quail *chimerae*, these cells migrate from the somites into the limbs although the tendons and intramuscular connective tissue apparently develop from the limb mesenchyme.

Only two papers (Bardeen and Lewis, 1901; Cihak, 1972) were found that described the morphology of the muscles in the embryonic lower limb. Bardeen and Lewis (1901) reconstructed the internal structures of four embryos (7mm, 9mm, 11mm, and 20mm) from which they described the differentiation of the extrinsic muscles. Their paper included illustrations of their models which resembled a superficial dissection. Unfortunately, the details concerning the muscles attachments were not apparent from the drawings and were not described. Cihak (1972) studied the ontogenesis of the intrinsic muscles from the serial sections of embryonic and fetal feet and described some of their attachments.

Summary

The embryonic development of the human foot has been studied for more than a century. Certain aspects, such as chondrification and joint formation have been documented extensively. Other aspects, such as the relationships and attachments of muscles and the mechanisms causing the postural changes have not yet been well defined.

Generally speaking, the literature predating 1950 provides a poor account of the methodology used. Furthermore, the observations from these earlier works are supplemented by very few illustrations or photographs, relying for the most part on cumbersome and often confusing written descriptions of the embryonic development of the human foot.

B. PHYLOGENETIC DEVELOPMENT OF THE HUMAN FOOT

> Man's foot is all his own. It is unlike any other foot. It is the most distinctly human part of the whole of his anatomical make-up. It is a human specialization and whether he be proud of it or not, it is his hall-mark and so long as Man has been Man and so long as he remains Man, it is by his feet that he well be known from all other members of the animal kingdom. (Jones, 1949: 2)

It is apparent from the literature that many authors consider that the structure, function and dysfunction of the human foot cannot be well understood without a basic understanding of its phylogeny (Morton, 1942; Jones, 1949; Giannestras, 1973; Jaffe and Laitman, 1982). The evolutionary history of the human foot has been reconstructed through the contributions of:

1. paleontology (Leakey, 1960; Leakey and Hay, 1979; Jaffe and Laitman, 1982; Latimer *et al.*, 1982; Conroy and Rose, 1983; Susman, 1983; Trinkaus, 1983)
2. comparative vertebrate anatomy (Morton, 1924 and 1942; Straus, 1927; Keith, 1929; Schultz, 1930; Elftman and Manter, 1936; Olson and Seidel, 1983; Susman, 1983)
3. and embryology (Leboucq, 1882, cited in Jones, 1949; Straus, 1927; Cihak, 1972; Crelin, 1983).

Most of the writers have focused on its more recent ancestry. To this end, Jaffe and Laitman (1982) have provided a comprehensive overview on the evolution of the primate foot. Other writers have followed the phylogeny of the vertebrate lower limb through the evolutionary series, beginning with its hypothetical origin in the lobe-fin fish (Morton, 1942; Giannestras, 1973). Unfortunately, most of

these descriptions are based on conjecture and are largely unsubstantiated.

The Fossil Record

The only direct evidence of the phylogeny of the human foot is the fossil pedal material. The more important findings include: the nearly complete foot of Australopithecus Habilis found at Olduvai Gorge in Tanzania, dated at approximately 1.8 million years ago (Leakey, 1960); the preserved footprints of early Australopithecines found at the Laetolil Beds in northern Tanzania, dated at approximately 3.7 million years ago (Leakey and Hay, 1979); and most recently, the fossils of Australopithecus Afarensis recovered from the Hadar formation in Ethiopia, dated at approximately 3.5 million years ago (Latimer *et al.*, 1982). Both the Olduvai foot and the Laetolil footprints showed a well-developed medial longitudinal arch and the absence of hallucial divergence, which are considered to be distinctively human characteristics. In contrast, the Hadar foot bones demonstrated marked convexity of the metatarsal surface on the first cuneiform, which was thought to indicate the abduction capacity of the first metatarsal. Susman (1983) hypothesized that the Hadar foot material represented a "missing link" between the apes and later hominids.

From reviewing the fossil record from 70 million years ago to 5 million years ago, Conroy and Rose (1983)

considered that the most significant change in the early evolution of the foot was the progressive migration of the talus over the calcaneus and the concommitant loss of the weight-bearing articulation between the fibula and the calcaneus.

Comparative Studies

Despite the information provided by the fossil material, the gaps in the fossil record remain large. Therefore, many workers have based their interpretation of the evolution of the human foot upon comparative studies, in particular the feet of living nonhuman primates. The striking similarity between the Hadar fossils and the chimpanzee foot was the justification used by Susman (1983) to utilize the chimpanzee as a model of the ancestral hominid foot.

Many writers have drawn attention to the features of the human foot that make it unique and distinquish it from all the nonhuman primates:

1. the well-developed transverse and longitudinal arches
2. the rigid ligamentous support
3. the parallel first and second metatarsals
4. the increased length of the first metatarsal which permits even distribution of forces between the first and second metatarsal heads
5. the relatively short outer four toes
6. the untwisted metatarsophalangeal joints so that the

toes face directly plantarward

(Straus, 1927; Schultz, 1930; Elftman and Manter, 1936; Morton, 1942; Olson and Seidel, 1983).

These workers shared the belief that, based on comparative pedal anatomy, the human foot evolved from a flat, prehensile organ with a short, divergent hallux to a semi-rigid arched structure with an adducted hallux which was specialized for habitual bipedal locomotion.

Embryonic Studies

In addition to comparative studies, other indirect evidence of the evolution of the human foot comes from investigations of the embryonic development of the human foot. The basis for this evidence is the recapitulation theory, popularized by Hæckel in the 1800's, which postulated that "ontogeny recapitulates phylogeny" (Gould, 1977). The essence of this theory is that individual development repeats ancestral conditions. Several workers have observed the striking resemblance between the features seen in the early stages of human embryonic development and the conditions seen in adult primates. Therefore, they felt justified in using the recapitulation theory as a guiding principle and extrapolated the evolution of the human foot from its embryonic development (Leboucq, 1882, cited in Jones, 1949; Cummins, 1926; Straus, 1927). According to Straus (1927: 94):

> The fact that the feet of man and other primates are much more alike in the early stages of development

> than they are later in life, most of their adult differences being produced through divergent growth, points strongly to a basal type of foot from which the variously specialized feet of all primates developed phylogenetically as well as ontogenetically.

Although Gould (1977) claimed that the recapitulation theory had "utterly collapsed" by the end of the 1920's due to its racist implications, there are several instances where workers in recent years have applied the concept of this theory to infer the evolution of the human foot. Cihak (1972) concluded from his study of the embryonic development of the skeleton and intrinsic muscles of the foot and hand that the ontogenesis of the musculoskeletal structures presents all the features of form change which took place in the course of phylogenesis. However, he pointed out that the term recapitulation could not be conceived to cover the reiteration of conditions in adult species from phylogenesis. Similarly, Crelin (1983) was convinced that the ontogeny of the human foot is a synopsis of its phylogeny. Perhaps the best definition of the recapitulation theory as it has been used in recent years was provided by Olson and Seidel (1983: 323) who wrote:

> The structural stages in the transformation of the human embryo reproduce the embryonic form of certain ancestral types at similar stages of development.

Summary

The various theories regarding the phylogeny of the human foot have come from the fields of paleontology, comparative anatomy and embryology. However, the only

conclusive evidence of the history of the human foot comes from pedal fossil remains.

C. BIOMECHANICAL FUNCTION AND DYSFUNCTION OF THE FOOT

The literature contains numerous general accounts of the biomechanical function and dysfunction of the human foot (MacConaill and Basmajian, 1969; Mann, 1973; Hutton, Stott and Stokes, 1976; Hlavak, 1977; Rosse, 1979; Frankel and Nordin, 1980; Sammarco, 1980; and Cailliet, 1983). In addition, there are reports that have focused on specific aspects of biomechanical function and dysfunction including:

1. gait (Saunders, Inman and Eberhart 1953; Stolov, 1979; Inman, Ralston and Todd, 1981)
2. muscle function in the lower limb (F. W. Jones, 1949; Basmajian, 1967)
3. mechanisms supporting the longitudinal arches (R. Jones, 1941; Lapidus, 1943; Hicks, 1954; Basmajian, and Stecko 1963)
4. the physiology of the joints (Manter, 1941; Barnett and Napier, 1952; Hicks, 1953; Isman and Inman, 1969; Kapandji, 1970; Jahss, 1982).

Other accounts have dealt with specific biomechanical disorders including:

1. pes planus (Giannestras, 1973; Kolker, 1973; Rose, 1982)
2. pes cavus (Hsu and Imbus, 1982)
3. metatarsal pathomechanics (Morton, 1942; Viladot, 1982)
4. varus deformities (Hadden, 1974)
5. torsional abnormalities (LaPorta, 1974; Aston, 1979)
6. forefoot-hindfoot malalignment (Duckworth, 1983)
7. sports injuries (Brody, 1980; Coker and Arnold,1982;

McReynolds, 1982).

The biomechanical function and dysfunction of the foot has direct bearing on the embryonic development of the foot for two reasons. Firstly, congenital deformities of the foot such as talipes equinovarus disrupt the biomechanical function of the lower limb (Turco, 1981). Secondly, many disorders that are described as biomechanical in nature have been attributed in part to subtle congenital variations in the skeletal system (Isman and Inman, 1969).

Pes Planus

Of all the biomechanical disorders of the foot, pes planus appears to have received the most attention. Many etiological factors have been identified, some of which are congenital. For example, a tarsal coalition, resulting from incomplete separation between two bones during embryonic development (Gardner *et al.*, 1959) is thought to be one of the causes of congenital pes planus (Salter, 1981). Kolker (1973) drew attention to three other congenital factors which could account for other varieties of pes planus: equinus of the ankle due to a congenitally short gastrocnemius; forefoot varus which he attributed to incomplete ontogeny; and calcaneal valgus which he attributed to excessive ontogeny. In addition, Kolker (1973) described other biomechanical disorders which he attributed to errant ontogenetic development: calcaneal varus (lack of ontogeny) and forefoot valgus (excessive ontogeny).

Axes of Joint Rotation

Studies of cadaveric limbs have revealed considerable variation in the axes of rotation of the ankle, subtalar and transverse tarsal joints (Manter, 1941; Hicks, 1953; Isman and Inman, 1969). According to these workers, the axis of rotation of the ankle joint has a slight downward inclination from medial to lateral, passing just distal to the tips of the malleoli. Isman and Inman (1969) found that the angle between the ankle joint and the long axis of the tibia in the coronal plane varied from 68 to 88°, with a mean of 80°. Inman (1969) demonstrated that the inclination of this axis causes the foot to deviate medially (adduct) during plantar flexion and laterally (abduct) in dorsiflexion. When the axis is close to the horizontal, this displacement is neglible. However, the further the axis moves from the horizontal, the more pronounced is the displacement.

Barnett and Napier (1952) observed that when the ankle is plantar flexed, the talus rotates medially in the horizontal plane in order to maintain joint congruity within the mortice. As a result of this medial rotation, the fibula appears to be situated more posteriorly in relation to the talus when the ankle is plantarflexed.

Studies have shown that the inclination of the axis of the subtalar joint shows even greater individual variation than the ankle. Isman and Inman (1969) reported that in the sagittal plane, the axis of rotation varied from 20 to 68°,

with a mean of 41°. Manter (1941) found a similar mean angle of 42° although the range was smaller, from 29 to only 47°. Inman (1969) explained that this axis of rotation permits the subtalar joint to function as an oblique hinge when the limb is weight-bearing, coordinating axial rotation of the leg above, with inversion and eversion of the hindfoot below. Consequently, in weight-bearing, lateral rotation of the leg is coupled with subtalar inversion while medial rotation of the leg occurs with subtalar eversion. Inman (1969) also found that the ratio of subtalar motion to axial rotation of the leg varies with the angle of inclination. When the axis of rotation is closer to the horizontal, as seen in the foot with pes planus, a large amount of subtalar motion is coupled with a small amount of axial rotation of the leg. Conversely, when the axis of rotation is closer to the vertical, as in the foot with pes cavus, a small amount of subtalar motion is coupled with a large amount of axial rotation of the leg.

The subtalar axis of rotation is also situated obliquely in the horizontal plane. Isman and Inman (1969) found that the angle between the axis of rotation and the long axis of the foot varied from 4 to 47° with a mean of 23°. Manter (1941) reported a range of 8 to 24° with a mean of 16°. Inman (1969) pointed out that as a result of this obliquity, inversion at the subtalar joint is associated with adduction of the forefoot whereas subtalar eversion occurs with abduction of the forefoot. Furthermore, the

greater the angle between the subtalar joint axis and the long axis of the foot, the greater is the amount of forefoot adduction and abduction associated with subtalar inversion and eversion respectively. These observations concurred with the reports by Manter (1941) and Hicks (1953). According to these workers, rotation about the oblique subtalar axis brings about positional changes of the foot in three planes i.e. inversion at the subtalar joint causes adduction and plantar flexion of the whole foot whereas subtalar eversion brings about abduction and dorsiflexion.

The subtalar joint has also been found to have a direct influence on the tranverse tarsal joint (Cailliet, 1983). This joint is actually comprised of two articulations: the talonavicular and calcaneocuboid joints. Since the calcaneus is common to both the subtalar (i.e. talocalcaneal) and calcaneocuboid joints, the function of the transverse tarsal joint is essentially under the control of the subtalar joint. Mann (1973) explained that when the subtalar joint is inverted, the axes of rotation of the talonavicular and calcaneocuboid joints are divergent which causes motion at the transverse tarsal joint to be suppressed. This may account for the rigidity seen in talipes equinovarus. Conversely, when the subtalar joint is everted, the axes of rotation of the talonavicular and calcaneocuboid joints are parallel, permitting motion at the transverse tarsal joint.

Therefore, the axes of rotation of both the ankle and the subtalar joints account for two postural patterns seen

in the well-balanced foot:

1. plantar flexion/inversion/adduction
2. and dorsiflexion/eversion/abduction (Turco, 1981).

Talipes equinovarus (clubfoot), a congenital postural deformity, actually represents a fixed exaggeration of the first pattern. Conversely, the second pattern predominates in talipes calcaneovalgus (reverse clubfoot) (Giannestras, 1973).

Muscle Function

The preceding discussion has explained how the function of the foot is affected by the various axes of joint rotation. The other important influence is the relative power of the individual muscles coupled with the relationship of their tendons to the joint axes. The greater the distance between the site of attachment of a tendon and a joint axis, the greater is its leverage which in turn results in greater influence on that joint (Jahss, 1982; Rose, 1982). These writers also pointed out that, with the exception of the calcaneal tendon, all the extrinsic tendons of the foot cross the ankle, subtalar and transverse tarsal joints. Therefore, contraction of these muscles has a concommitant influence on at least three joints in the foot. Another important biomechanical consideration is that the tendon-axis relationships change throughout the range of motion of all joints. As a result, the action of a muscle on a joint depends on the position of the joint on which it is

acting.

Jahss (1982) explained how the function of the tibialis anterior varies with the position of the subtalar joint. When the calcaneus is inverted, as in talipes equinovarus, its ability to invert the subtalar joint is increased. Conversely, when the calcaneus is everted, as in a valgus deformity of the heel, the distal attachment of the tibialis anterior tendon is situated lateral to the subtalar axis, and the muscle functions as a subtalar evertor.

The function of the triceps surae (i.e. the soleus and the two heads of gastrocnemius), which is both a plantar flexor of the ankle and an invertor of the subtalar joint, has also been found to vary with the posture of the subtalar joint (Jahss, 1982). When the heel is positioned in varus, the calcaneal tendon is situated further from the subtalar axis, thereby increasing its inversion power. Conversely, as the calcaneus goes into progressive valgus, the attachment of the triceps surae is carried laterally in relation to the subtalar axis, thereby reducing its inversion power. According to Rose (1982), in the severe valgus heel the triceps surae actually becomes an evertor of the subtalar joint.

Turco (1981) pointed out that the triceps surae and the tibialis posterior are the only extrinsic muscles that attach to the calcaneus and that their synergistic function is to simultaneously plantar flex the ankle and invert the subtalar joint. Therefore, in talipes equinovarus, the same

muscles that are causing the equinus (plantar flexion) deformity are also contributing to the varus (inversion) deformity of the heel (Jahss, 1982).

Summary

Two important aspects concerning the biomechanical function of the human foot are:

1. the axes of joint rotation
2. and the relative power of each individual muscle coupled with the relationship of its tendon to the joint axes (i.e. tendon-axis relationship)

Although the literature contains numerous studies of the biomechanics of the adult foot, no specific information was found pertaining to the embyronic foot.

D. CONGENITAL ANOMALIES OF THE FOOT

This section focuses on those congenital anomalies which various clinicians and researchers have attributed to "arrested embryonic/fetal development".

Talipes Equinovarus (Congenital Clubfoot)

Talipes equinovarus is a relatively common foot deformity, occurring in one or two per 1000 live births (Stewart, 1951; Salter, 1981). These statistics do not differentiate between unilateral or bilateral occurrences. Various studies have also found that the male to female ratio is approximately 2 to 1 (Stewart, 1951; Wynne-Davies, 1964a).

Talipes equinovarus occurs either as an isolated congenital deformity or as part of a more generalized group of musculoskeletal disorders associated with arthrogryposis, myelomeningocele or other congenital deformities (Turco, 1981). When it occurs as an isolated congenital anomaly, the deformity is either nonrigid or rigid. The latter is considered to be the true talipes equinovarus. The nonrigid clubfoot, which is sometimes described as positional equinovarus, can be manipulated into the anatomical position and is generally thought to be a consequence of intrauterine malposition (Lehman, 1980). In contrast, the rigid talipes equinovarus resists passive correction and its etiology is uncertain and controversial (Lehman, 1980). The literature described in this section pertains only to the idiopathic,

rigid, congenital talipes equinovarus and will be referred to simply as clubfoot.

There exists in the literature a disparity of opinions concerning the pathoanatomy and etiology of clubfoot. However, there appears to be a general consensus that the postural components of the deformity include:

1. forefoot adduction and inversion (varus)
2. calcaneal inversion (varus) at the subtalar joint
3. and equinus at the ankle joint

(Hauser, 1966; Lehman, 1980; Salter, 1981; Turco, 1981). In addition, some patients present with a cavus component caused by plantar flexion (equinus) of the forefoot (Turco, 1981).

Although the majority of the studies (e.g. Hauser, 1966; Huurman, 1978; Lehman, 1980) agree that both the skeletal and muscular structures are affected in clubfoot, the descriptions of the precise pathoanatomy are varied and often contradictory. Huurman, (1978) and Turco (1981) attributed the discrepant reports to several factors. Firstly, some researchers have failed to differentiate the true talipes equinovarus from the less severe positional equinovarus or the clubfoot associated with multiple congenital anomalies. Secondly, there is great disagreement as to which are the primary defects as opposed to the secondary adaptive changes. Thirdly, the varied and conflicting reports of the pathology seen during surgery or on radiographs suggest that pathological changes may vary

between individuals presenting with clubfoot. Finally, since talipes equinovarus is not the cause of fetal or infant mortality, postmortem specimens with clubfoot as an isolated deformity are not readily available. Instead, most postmortem dissections have been performed on premature fetuses in which clubfoot is only one component of a more generalized congenital disorder (e.g. see Bechtol and Mossman, 1950).

The most commonly reported skeletal anomaly in the clubfoot is deformity of the talus. The various reported findings include: increased medial deviation of the talar neck (Irani and Sherman, 1963); deviation of the talar neck in the plantar direction (McKay, 1982); talar neck longer than normal (Waisbrod, 1973); foreshortened talar neck and absence of the usual constriction (Irani and Sherman, 1963; Huurman, 1978; Turco, 1981); the long axis of the talar neck is more horizontal than seen in the normal neonatal foot (Kaplan, 1972); and absence of the normal concavity of the trochlear surface (Kaplan, 1972). Turco (1981) pointed out that the anterior portion of the talar trochlea is relatively broader in the clubfoot, posing a bony block which contributes to the persistance of equinus at the ankle. He attributed this to the fact that the trochlea had never fully entered the ankle mortice and therefore never had the opportunity to be moulded to fit it.

Pathological changes in the calcaneus have also been recorded including: smaller proportions (Irani and Sherman,

1963: Schlicht, 1963); concavity of the medial surface of the calcaneus in the horizontal plane (Irani and Sherman, 1963; Schlicht, 1963; Ippolito and Ponsetti, 1982); and inward rotation of the posterior 1/3 of the calcaneus (Schlicht, 1963).

Regarding the relative positions of the talus and calcaneus, there appears to be a general agreement that in clubfoot, the calcaneus is inverted below the talus in the coronal plane (Stewart, 1951; Irani and Sherman, 1963; Ippolito and Ponsetti, 1980). In addition, Turco (1981) and McKay (1982) described horizontal rotation of the calcaneus, pivotting around the interosseus ligament, which displaces the anterior part of the calcaneus medially and under the head of the talus while the posterior part moves laterally and closer to the fibular malleolus.

Kite (1939) devised a method of quantifying the talocalcaneal relationship in the horizontal plane using radiographs. In the anteroposterior (AP) view, the long axis through the talus and the long axis of the calcaneus converge posteriorly, forming the talocalcaneal (Kite's) angle. According to Huurman (1978), in the normal foot the long axis through the talus passes through the first metatarsal and the long axis of the calcaneus aligns with the fifth metatarsal, creating an angle of 20° to 40°. In the clubfoot, this AP talocalcaneal angle is reduced, sometimes to 0°.

The talocalcaneal relationship can also be assessed from lateral view radiographs. In this case, the angle is derived from a line drawn through the longitudinal axis of the talus at its midpoint and a second converging line is drawn along the plantar surface of the calcaneus. Heywood (1964, cited in Huurman, 1978) reported that this angle measures between 35° to 50° in the normal standing lateral projection. In the clubfoot, these two lines are nearer to being parallel (Huurman, 1978).

McKay (1982) was convinced that horizontal rotation of the calcaneus in clubfoot accounted for the apparent posterior position of the fibular malleolus. Hosking and Scott (1982) also acknowledged posterior displacement of the fibular malleolus in relation to the calcaneus. However, they attributed it to lateral rotation of the anterior part of the talus in the horizontal plane. Other interpretations of the apparent posterior displacement of the fibular malleolus include lateral rotation of the ankle mortice (Wynne-Davies, 1964b) and tethering of the fibular malleolus (Swann *et al.*, 1969)

The bones of the middle region of the clubfoot are not noticeably different from those of the normal foot in size or shape. However, medial displacement of the navicular on the talar head has often been reported in clubfoot (Turco, 1981; McKay, 1982). Similarly, several sources described medial displacement of the cuboid in relation to the calcaneus (Bechtol and Mossman, 1950; Schlicht, 1963;

Ippolito and Ponsetti, 1980; McKay, 1982).

The medial deviation of the navicular and cuboid accounts in part for the adduction of the forefoot seen in clubfoot. However, it is generally thought that the majority of the forefoot adduction can be attributed to the deviation of the metatarsal shafts toward the medial side of the foot. Wynne-Davies (1964b) pointed out that the first cuneiform articulating with the medial aspect of the base of the first metatarsal is another contributing factor. There have also been reports that the first metatarsal is shorter than normal in clubfoot (Schlicht, 1963; Wynne-Davies, 1964b; Lehman, 1980; Turco, 1981).

Some investigators have developed theories regarding the etiology of clubfoot based on the bony abnormalities that they have seen. For example, Irani and Sherman (1963) concluded that the primary etiological factor in clubfoot is an abnormal cartilage anlage for the talus due to a primary germ plasm defect. Similarly, Waisbrod (1973) concluded that the problem was probably blastemal in origin. However, Turco (1981) contended that the various bony abnormalities are secondary and adaptive.

Similarly, the opinions vary as to whether or not the abnormalities that are seen in the muscles are the primary defect or represent an adaptive change due to disuse. General observations regarding the extrinsic musculature include reduced muscle bulk, contracted posteromedial muscles and overstretched, weak peroneal muscles

(Wynne-Davies, 1964b). The theories that have implicated the extrinsic muscles as the cause of clubfoot generally fall into one of the following four categories:

1. abnormal muscle development due to vascular insufficiency (Atlas, *et al.*, 1980)
2. abnormal muscle development due to a faulty innervation (Isaacs *et al.*, 1973; Handelsman and Badalamente, 1981; Gray and Katz, 1981)
3. retracting fibrosis (Ippolito and Ponsetti, 1980)
4. abnormal muscle function due to aberrant attachment of tendons (Stewart, 1951; Schlicht, 1963; Ippolito and Ponsetti, 1980; Turco, 1981).

According to Salter (1981), genetic factors account for about 10% of clubfoot occurrences. Similarly, Wynne-Davies (1964a) reported that, based on the notes on 340 patients, the chances of a second child in the same family having this deformity are 24X greater than the general population. She formulated the theory that clubfoot is partly genetic and partly environmental, caused by the following mechanism:

1. genetic factors disturb the formation of connective tissue causing the foot to be
2. abnormally mobile and therefore vulnerable to
3. adverse environmental factors *in utero* related to abnormal pressure or position in the uterus.

She added that the consequence of the deforming forces depends on when they are applied during the prenatal period. For example, if the adverse forces are applied during the

later stages of development, a less severe congenital foot deformity will result.

Hauser (1966) also attested to the interdependence of genetic and environmental factors. He stated that genetically inherited traits predispose the embryo to the development of an anomaly when exposed to certain environmental changes which might ordinarily not be harmful.

Other investigators have maintained that adverse environmental factors alone are to blame for clubfoot. Hippocrates has been credited with developing this theory. In approximately 400 B. C. he wrote:

> "Children have become crippled in the following way. If the womb is narrow at that part in which the crippling is produced, it is inevitable that the body moving in a narrow space should become crippled in that part." (cited in Brown, 1967: 12)

The proponents of this theory contend that fetal malposition and mechanical forces related to constrained intrauterine space is the most common cause of idiopathic foot and leg deformities at birth (Parker, 1887, cited in Hauser, 1966; Hoffa, 1902, cited in Hauser, 1966: Nagura, 1956, cited in Hauser, 1966; Browne, 1967; Aston, 1979). Some of these workers considered that oligohydramnios could also be a contributing factor.

Other workers have implicated "arrested prenatal development" as the underlying cause of clubfoot. According to Hauser (1966), this theory was first advanced by Heuter in 1863. In the years that followed, this theory fell into disfavour due to the writings of Bessel-Hagen (1889, cited

in Bohm, 1929) and his supporters who claimed that at no time does the embryonic foot resemble a clubfoot. In 1929, Bohm lent new credibility to the theory of arrested development. By reconstructing the lower limbs of four specimens at 18, 23, 35 and 57mm CRL, Bohm (1929) demonstrated the changing size, shape and relationships of the skeletal elements. He observed the striking similarity between the skeletal elements of the embryonic foot and the clubfoot of a seven month fetus and reasoned that the deformity results from an arrest of development due to a primary endogenous disturbance of the embryo.

Subsequent investigators have also supported the theory of arrested development (e.g. Scherb, 1931; Martinez-Cuadrado and Gonzalez-Santander, 1967). Most recently, Victoria-Diaz and Victoria-Diaz (1984) proposed that noxious industrial substances can disrupt the growth phases of the developing bones, producing congenital foot deformities. They also thought that the nature of the deformity produced depended on the stage of development that the noxious substance was introduced and the duration of contact. Unfortunately, they did not identify any particular teratological agents.

Numerous animal studies have examined various teratological factors and have demonstrated that deformities resembling clubfoot can be induced by: various dietary defiencies in pregnant rats (Warkany *et al.*, 1943; Asling, 1955; Nelson *et al.*, 1956); irradiation of mouse embryos,

(1960); the administration of retinoic acid (Vitamin A acid) to pregnant rats (Kwasigroch, 1980). These animal studies also demonstrated that the susceptibility of the embryo to the deforming agent depended on when it was administered. However, considering that the human foot is unlike any other foot in the animal kingdom, it is questionable whether any animal model can represent adequately its prenatal development.

Summary

Clinicians and researchers have disagreed about the etiology and pathoanatomy of clubfoot since the time of Hippocrates. Although numerous theories have been proposed and investigated, a primary etiological factor has not yet been identified. One of the principal contributing factors is the disparity of opinions as to which of the skeletal and muscle abnormalities represent primary defects in contrast to secondary adaptive changes.

A thorough and convincing investigation of the etiological theory of arrested embryonic development first requires a comprehensive understanding of the musculoskeletal development in the embryonic foot. Until this process has been well documented, this theory can be neither confirmed nor disproved.

Other Congenital Foot Anomalies

The various postural components of clubfoot are also seen as isolated congenital anomalies. For example, metatarsus adductus has been described as 1/3 of a clubfoot (Wynne-Davies, 1964b). In this congenital anomaly, the forefoot is adducted and inverted but the hindfoot is not involved. The congenital anomaly described as forefoot varus presents with only inversion of the forefoot (Kolker, 1973).

Morton (1942) was the first to bring attention to the congenitally short first metatarsal as an isolated anomaly. Another congenital variation of the first metatarsal is metatarsus primus varus, in which the first metatarsal is deviated away from the second metatarsal (Salter, 1981).

Isolated congenital postural anomalies affecting the hindfoot are: calcaneal varus, in which the calcaneus is inverted in relation to the talus; and equinus, which in some situations can be attributed to a congenitally short gastrocnemius (Kolker, 1973).

E. SERIAL RECONSTRUCTION TECHNIQUES

Serial reconstruction is a process whereby the information contained in serial sections is reassembled as a scaled model to demonstrate the spatial relationships of the various components. Comprehensive overviews of the various methods and applications of serial reconstruction have been written by Ware and LoPresti (1975) and Gaunt and Gaunt (1978). There are basically four categories of serial reconstruction:

1. graphical (His, 1880, cited in Ware and LoPresti, 1975; Kastchenko, 1886, cited in Gaunt in Gaunt, 1978; Odner, 1911; Peter, 1922; Halpern, 1953; Barnett, 1956; Dixon and Howarth, 1958; Yamada and Yoshida, 1971; Dunn, 1972)
2. solid (Born, 1876, cited in Bardeen, 1901 and 1905; Bardeen and Lewis, 1905; Gage, 1907; Schaeffer, 1911; Wallin, 1913; Straus, 1927; Green, 1937; Boyer, 1948; Bleschschmidt, 1954; Huson, 1969; Olivier, 1962; Martinez-Cuadrado and Gonzalez-Santander, 1967; Jergensen, 1971; Cihak, 1972)
3. transparent (Kerr, 1902, cited in Gaunt and Gaunt, 1978; His, 1904, cited in Gaunt and Gaunt, 1978; Senior, 1929; Brown and Arnott, 1971; Gaunt and Gaunt, 1978)
4. serial section cinematography (Reicher, 1907, cited in Gaunt and Gaunt, 1978; Hegre and Brashear, 1946; Bush, 1952; Hegre, 1952 and 1967; Ware and Levinthal, 1971; Levinthal and Ware, 1972 and 1975)

Graphical Reconstruction

According to Ware and LoPresti (1975), the first type of graphical reconstruction was produced by His in 1880 as part of his study of human embryology. His' method creates a single composite drawing which is similar to a contour map.

A restriction imposed by His' method is that the reconstructed image can only represent one view, that is perpendicular to the plane of sectioning. This limitation was overcome by the development of the various techniques which produce perspective or oblique view drawings from almost any angle with respect to the plane of sectioning (Odner, 1911; Peter, 1922; Halpern, 1953; Barnett, 1956; Dixon and Howarth, 1958; Dunn, 1972).

Stereoscopic reconstruction is an extension of graphical reconstruction in which two views of the same object are drawn or photographed from slightly different angles (Yamada and Yoshida, 1971). When the paired contour drawings are viewed with a stereoscope, the two images are superimposed, and the impression of depth is created. However, Gaunt and Gaunt (1978) were of the opinion that stereoscopic reconstruction offers no advantage over perspective reconstructions and are more time-consuming to produce.

Graphical reconstructions can also be produced with the aid of computers which can generate an image from any desired view onto a graphics display terminal (Gaunt and Gaunt, 1978). Any image displayed on the terminal can then

be printed by a plotter onto paper.

Solid Reconstruction

According to Gaunt and Gaunt (1978) solid reconstruction was pioneered by Born in 1876. Like His, he used a *camera lucida* to project the serial sections and then draw onto paper magnified enlargements of the structures to be analyzed. Unlike His, each of the series of tracings was subsequently reproduced onto a plate of wax from which the profiles were cut, stacked and adhered together, producing a solid three-dimensional model (Bardeen, 1901).

Born (1876) manufactured his own wax plates by pouring molten wax onto hot water and allowing them to cool slowly (Bardeen, 1901). A variety of other opaque materials have been used in solid reconstructions including blotting paper (Gage, 1907), wax-impregnated blotting paper or wood pulpboard (Green, 1937), polystyrene sheets (Pedler and Tilly, 1966), cardboard (Huson, 1969), plastic (Cihak, 1972) commercially available dental modelling wax, balsa wood, pine wood, tin foil, leather, cork, and gelatin (Gaunt and Gaunt, 1978).

Although the choice of medium for solid reconstruction is highly variable, a fundamental requirement of any plate construction method is that the thickness of the component plates must be in proportion to the section thickness and the magnification. Otherwise, some degree of lengthening or foreshortening will result in the final solid model.

Variations on the basic method of solid reconstuction developed by Born have been reported. Schaeffer (1911) devised the dissectible blotting paper model made up of segments that were hinged together and which opened up like the pages of a book to reveal the internal organization of the structure. Boyer (1948) and Bleschschmidt (1954, cited in Gaunt and Gaunt, 1978) used wax plates to construct negative models which served as hollow molds that were subsequently injected with a polymerizable plastic. After the plastic had hardened, the wax was removed, leaving a durable, heat resistant and unbreakable plastic model. In a similar fashion, Jergensen (1971) used Plexiglas plates to produce a negative model of the lumina in the liver which were subsequently filled with different coloured fluids to reconstruct the portal tracts.

Levinthal and Ware (1975) pointed out several shortcomings of solid models. They are more time-consuming to construct, require far more space than graphical reconstructions for storage and are more difficult to transport. Unless the solid model is dissectible, it is not possible to view the internal organization of the structure. Also, they do not lend themselves to quantitative measurements as are properly constructed two-dimensional projections. Graphical reconstructions can more easily be reproduced for publication because their original form is two-dimensional. These authors concluded that despite the often striking products, solid models have consistently

retained a second place to graphical reconstructions, except for some eductional purposes. However, it can be argued that after it has been constructed, a solid model can be viewed and photographed from any angle whereas a separate drawing is required for each view of a structure when using graphical reconstruction techniques.

Tranparent Reconstructions

Transparent models are a combination of graphical and solid reconstructions whereby the contours from each section are traced onto plates of glass or plastic. The thickness of the plates must be consistent with the section thickness and magnification in order to establish the correct proportion of depth in the reconstruction. Alternatively, the contours can be traced onto sheets of thin transparent plastic and then interleaved with spacers of correct thickness. The set of tracings are then stacked in register and viewed by transillumination, permitting the investigator to see through every structure and observe the internal organization from a wide range of views in one model (Gaunt and Gaunt, 1978).

As with solid plate reconstructions, various transparent materials have been used: glass (Kerr, 1902, cited in Gaunt and Gaunt, 1978); celluloid (His, 1904, cited in Gaunt and Gaunt, 1978); sheet celluloid or sheet gelatin (Senior, 1929); orthochromatic lithofilm (Brown and Arnott, 1971); and acetate sheets (Gaunt and Gaunt, 1978).

One problem with transparent plate models is reproducing them in a two-dimensional format for publication. Dunn (1972) suggested two solutions: either an artist's rendition of the investigators observations or a pair of stereophotographs of the transparent model.

Serial Section Cinematography

The essence of this procedure is to project onto a screen, in strict sequence, all the individual sections comprising a large series and to photograph each image onto cinematographic film. This technique gives the viewer the impression of being taken on a journey from one end of the specimen to the other. With this modality, depth is primarily viewed as a temporal dimension.

Reicher was the first to report on this method in 1907 (Gaunt and Gaunt, 1978). Since then, several workers have adopted this modality to demonstrate microanatomy because it avoids the labour involved in making graphical, solid or tranparent models (Hegre and Brashear, 1946; Hegre, 1952 and 1967; Bush, 1952; Ware and Levinthal, 1971; Levinthal and Ware, 1972 and 1975). However, this approach has limited appeal due to the requirements for a meticulous histological technique that will yield a large number of precisely aligned, uniform, high quality sections. Another disadvantage of serial cinematography is its limited value as a mode of communication. Only those with direct access to the film can benefit from the information it contains.

Furthermore, the cine film as a whole cannot be communicated in print as a two-dimensional image (Gaunt and Gaunt, 1978).

Maximizing the Accuracy of Serial Reconstructions

One of the fundamental requirements in any system of reconstruction involving serial sections is a reliable system of orientating the individual sections with each other. The images of the serial sections must be superimposed in the same relative positions as in the original block of tissue. There are two basic approaches to this problem: either the use of external markers or the method of best fit.

The concept of external markers was introduced by Kastschenko in 1887. He coated the edges of the precisely trimmed specimen block with carbon prior to sectioning. In this way, the outline of each paraffin section was retained throughout the histological processing (Ware and LoPresti, 1975). Since these outlines maintained a constant relationship to each other, they served as guideposts to bring the tracings or photomicrographs into register. Other workers have devised alternate methods to produce surface reference marks (Marshall, 1965; Gaunt and Gaunt, 1978).

A second category of external markers is the included reference which is a substance embedded with the specimen before sectioning. For example, Burston and Thurley (1957) incorporated nerve fibers into the paraffin block. A variation of this method involves drilling localizing holes

into the tissue block, perpendicular to the subsequent cutting plane, prior to sectioning (Dixon and Howarth, 1958; Gough, 1968).

According to Gaunt and Gaunt (1978) emminent workers such as Born, (1876), His (1880), Kastschencko (1887) and Strasser (1887) assembled some of their models without the aid of reference markers, using instead the method of best fit. To ensure the most reliable alignment, outlines of as many ancillary structures as possible, over and above those being directly investigated, should be included in the tracings to serve as additional points of reference (Gaunt and Gaunt, 1978).

Some workers think that there is always a degree of doubt concerning the accuracy of the tracings aligned without external markers (Ware and LoPresti, 1975; Gaunt and Gaunt, 1978). However, various techniques have been devised to facilitate and improve the accuracy of aligning the sections without reference marks (Bush, 1952; Hegre, 1967; Levinthal and Ware, 1972).

Gaunt and Gaunt (1978) stressed that the accurate alignment of serial tracings or serial micrographs requires that distortion of the tissue section is avoided or reduced to a low and constant minimum level. Therefore, the first prerequisite to serial reconstruction is an unbroken series of sections of identical thickness and with a minimum of creases, folds, tears or any other kind of derangement.

Patten and Philpott (1921) examined the amount of shrinkage of the specimen induced by different fixatives (bichromate solutions, 10% formalin, formol-alcohol and Bouin's fluid) and by the dehydration and paraffin infiltration procedures. The implication of shrinkage in serial reconstruction is that it causes displacement between the parts of the organ being reconstructed. The authors discovered that the total amount of shrinkage resulting from these procedures does not appear to vary significantly with the fixative used. However, the histological condition of the material fixed in a bichromate solution or Bouin's fluid was distinctly superior to that fixed in 10% formalin or formol-alcohol.

Patten and Philpott (1921) concluded that processing for light microscopy produces dramatic shrinkage, regardless of the fixative used, especially in younger embryos where the mesoderm is less compact. The reduction in crown rump length ranged from approximately 30% in 10mm embryos to 20% in 20 - 25mm embryos.

Error can also be introduced during the process of cutting and mounting the serial sections. Heard (1951) pointed out that the microtome knife can cause internal derangement especially when very thin wax sections are cut. Gaunt and Gaunt (1978) advocated that wax sections should be cut no thinner than 13μm to minimize the amount of distortion caused by the mounting process.

Other sources of error in serial reconstruction include: defective knowledge of the precise plane of section (Hjortsjo, 1954; Marshall, 1965); and spherical abberation which distorts the image that has been produced by the microprojector on the drawing surface (Hjortsjo, 1954).

Histological serial sections are subject to numerous types of relative distortion which cannot be controlled although they should be recognized. Consequently, the reconstructions based on these sections are prevented by many inescapable factors from being entirely exact. Hjortsjo (1954) advocated that one try to eliminate those sources of error which can be avoided but not to force this elimination so far that it is out of proportion to the remaining unavoidable sources of error.

Serial Reconstructions of Prenatal Lower Limbs

A review of the literature disclosed eight studies that have used serial reconstructions to investigate the prenatal development of the human foot (Schomburg, 1900, cited in Bohm, 1929; Bardeen and Lewis, 1901; Bardeen, 1905; Straus, 1927; Bohm, 1929; Olivier, 1962; Martinez-Cuadrado and Gonzalez-Santander, 1967; Huson, 1969). All of these workers used solid reconstruction techniques exclusively. Although none of the reports provided a detailed account of the method used, the majority made reference to Born's (1876, cited in Bardeen, 1901) method of reconstruction.

The study by Bardeen and Lewis (1901) was perhaps the most general. They reconstructed all the internal structures of four embryos (7, 9, 11 and 20mm CRL) from which they described the progressive maturation of the internal elements. The report included illustrations of the models which resembled a superficial dissection. Unfortunately, the details concerning the muscle attachments were not apparent from the drawings and were not described.

The remaining seven studies were based on the reconstructions of only the skeletal elements of the prenatal lower limb. Bardeen's (1905) study included five embryos (9, 11, 14, 33, and 50mm CRL) which focused on the maturation of the cartilaginous skeletal elements. Unfortunately, the orientation and relative positions of the skeletal elements were not readily apparent from the illustrations of the models and were not described in the text.

Straus (1927) made plaster reconstructions of the skeletons of the feet from an eight week embryo and a three month fetus as part of a larger study on the growth of the human foot and its evolutionary significance. Unfortunately, he recorded very few observations from these models and did not photograph or illustrate them.

Martinez-Cuadrado and Gonzalez-Santander (1967) wrote a brief report, containing three illustrations, based in part on the reconstructions of four limbs (14.5, 20.5, 46 and 64mm CRL). These workers were particularly concerned with

the changing relationships of the talus and calcaneus and concluded that talipes equinovarus occurs due to an interruption of normal development between the stages of 28mm and 46mm CRL.

Most recently, Huson (1969) reconstructed the skeletons of both feet of a 115mm CRL fetus. He observed that at this stage, the foot closely resembles the configuration of the adult foot. The only finding of particular note was that one of the feet demonstrated a talocalcaneal coalition. Therefore, his study contributed little to the understanding of the prenatal development of the foot.

The most extensive studies of the skeletal development in the prenatal foot were done by Bohm (1929) and Olivier (1962). Bohm reconstructed the lower limbs of four specimens (~~18,~~ 23, 35 and 57mm CRL). His report included two or three different photographic views of each model. Like Martinez-Cuadrado and Gonzalez-Santander (1967), his study focused on the changing talocalcaneal relationship and he also concluded that arrested embryonic development accounts for talipes equinovarus.

Olivier (1962) described the skeletal development of the embryonic foot from the reconstructions of five specimens (14, 17, 21, 27 and 34mm CRL). He included a large number of illustrations of his models, representing different views, which documented the changing shape and relationships of the skeletal elements.

O'Rahilly, who has coauthored more papers than anyone else on the subject of the prenatal development of the human foot, strongly advocated the use of serial reconstruction, although he himself never utilized the modality. In 1973, he wrote:

> Further careful studies are needed in order to assess the extent to which the normal prenatal position of the foot is or is not similar to clubfoot... A great need exists for careful, closely-graded reconstructions of both normal and abnormal developing feet.... The reconstruction illustrated at 115mm by Huson shows the benefit of such an approach as a basis for understanding the appearance of the foot at even one point of time in development....May their numbers increase! (p 23)

F. SUMMARY

The review of literature revealed that the objectives for studying the embryonic development of the human foot generally fell into one of three categories:

1. to understand better the early development of the foot
2. to investigate the theory of "arrested embryonic development" as the primary cause of congenital clubfoot (talipes equinovarus)
3. to interpret its phylogeny using the recapitulation theory as a guiding principal

The literature review also showed that although there is a general concensus as to chondrification and joint formation in the embryonic foot, there is much discrepancy in the reports concerning the relationships of the skeletal elements. These reports have been used to either support or refute the theories of "ontogeny as a recapitulation of phylogeny" and "arrested embryonic development". Unfortunately, the discrepancies between the various reports have only fueled the controvery associated with these issues. Also identified was a general lack of information pertaining to the relationships and attachments of muscles in the embryonic foot and the mechanisms responsible for the postural changes.

III. MATERIALS AND METHODS

Unless otherwise noted, the calibration bar included in the figures represents 0.5mm for the embryonic specimens and 50mm for the adult specimens.

A. EMBRYONIC SPECIMENS

The primary source of material used in this study was the R. F. Shaner Collection, located in the Department of Anatomy, University of Alberta. It consists of 109 human embryos and fetuses which were acquired between 1915 and 1975. All of the specimens have been processed for light microscopy using standard histological techniques including fixation, embedding in paraffin and serial sectioning. The sections have been mounted on glass slides and stained with hematoxylin and eosin. This collection was developed primarily by Dr. Shaner to study development in the thoracic region, accounting for the absence of lower limbs in many of the larger embryos.

The records for each specimen include the cataloque number, fixative, stain, section plane, section thickness and the year it was processed. In addition, the external appearance of many specimens was documented prior to processing by either a photograph or a drawing. However, the records contain very little information pertaining to either

the processing methods or the medical history.

The records also indicate that the method used to assess the relative maturity of these specimens was the measurement of the crown rump length (CRL) prior to processing. However, this measurement has been shown to vary according to the amount of flexion of the specimen and should not be regarded as a precise indication of the gestational age (Bagnall, Jones and Harris, 1975).

The fact that none of the specimens have been sectioned with reference markers had a direct bearing on this study. When these specimens are studied using reconstruction techniques, the method of "best fit" must be used to align the sections.

Serially sectioned specimens were considered appropriate for this study if they met the following criteria:

1. comprising a complete series of sections of the foot
2. possessing sufficient differentiation of the musculoskeletal structures in the foot to be identified by light microscopy
3. having adequate histological quality and a minimal amount of damage.

Consequently, embryos less than 20mm CRL were found to be unsuitable because the internal structures of the foot were not sufficiently developed to be studied. Many of the larger embryos were also unsuitable because the lower limbs had been removed. As a result of these limiting factors, only

six embryos were considered suitable for use in this study.

With the exception of embryo XXI where Bouin's fixative had been used, the specimens had been fixed in formalin. Both feet were intact in only three specimens. Therefore, to help establish some degree of consistency, and also because the sectional planes were more appropriate, it was resolved to make observations principally from the right foot, except for embryo XXIII where only the left foot was intact (see Table 1).

Prior to studying the sectioned specimens, each of the glass slides was cleaned with methyl alcohol and any excess mounting medium was removed from the cover slips. Several of the slides required restoration because the mounting medium had crystallized around the periphery of the cover slips, obscuring the view of relevant structures. The restoration process entailed dissolving the crystalized medium with xylene and resealing the edges of the cover slip with Canada Balsam.

Using the criteria defined by O'Rahilly *et al.* (1957), the six specimens were "staged" to assess their relative maturity based on the chondrification in the foot rather than the CRL. It was determined that these embryos represented the last four stages of embryonic development (i.e. stages 20 through 23) with the approximate age range being between 40 and 48 postovulatory days (based on Streeter, 1951). Stages 21 and 23 were exemplified by one embryo each whereas stages 20 and 22 were each represented

TABLE 1. SPECIFICATIONS PERTAINING TO EMBRYONIC SPECIMENS

Embryo #	Shaner Catalogue #	Year Processed	CRL (mm)	Postovulatory Age in Days (Streeter, 1951)	Section Plane through Foot	Section Thickness (um)	Mode of Investigation	Comments
XXa	H81	1957	23.5	40-42	sagittal (R & L)	20	-trans model -sections	-fully intact lower limb
XXb	H17	1928	21.7	40-42	coronal (R & L)	N/A	-sections	-lightly stained
XXI	H104	1975	22	42-44	R-coronal L-oblique	10	-trans model -sections	-sections behind calcaneus damaged
XXIIa	H35	1942	25.5	44-46	R-horizontal L-coronal	40	-wax model -trans model -sections	-no sections above R mid-leg -L-only sections of hindfoot
XXIIb	H101	1966	28.5	44-46	sagittal (R & L)	20	-sections	-toes damaged -lightly stained
XXIII	H107	1966	34	46-48	L-horizontal	20	-trans model -sections	-not every section mounted -toes damaged

trans, transparent. R, right. L, left.

by two embryos (see Table 1). Although it was appreciated any two embryos cannot be identical, there was no clear evidence to indicate that one specimen was more advanced than the other of the same developmental stage.

The six embryos of the Shaner Collection were assigned new identification numbers for this study, based on their stage of development. For example, the two stage 20 embryos (Shaner Collection numbers H81 and H17) were designated as embryos XXa and XXb respectively. Using this system, the relative maturity of each embryo is apparent from its identification number. Table 1 shows the conversion from the Shaner catalogue number to the developmental identification number used in this study.

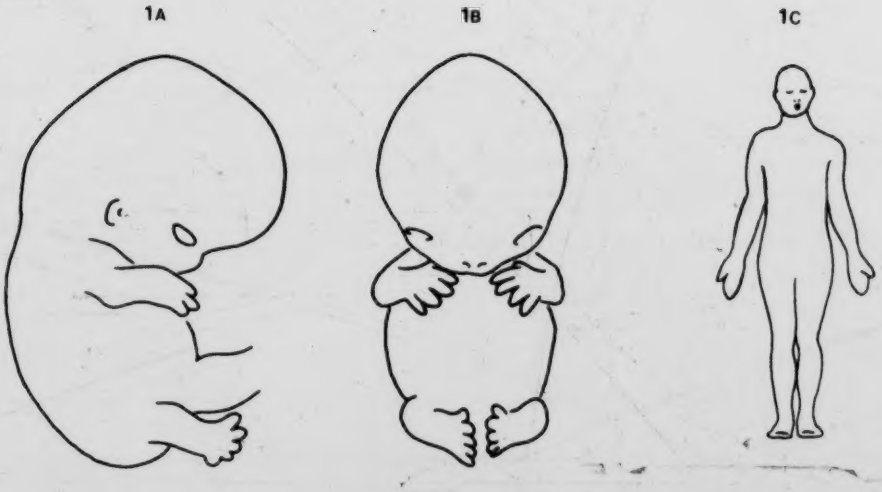
To understand the plane of section associated with each foot, it must first be appreciated that the position of the embryonic lower limb is not the same as the standard anatomical position (Fig 1). However, for simplicity, the sectional plane through the foot of each specimen will be described as though the foot was in the anatomical position (see Table 1 and Fig 2).

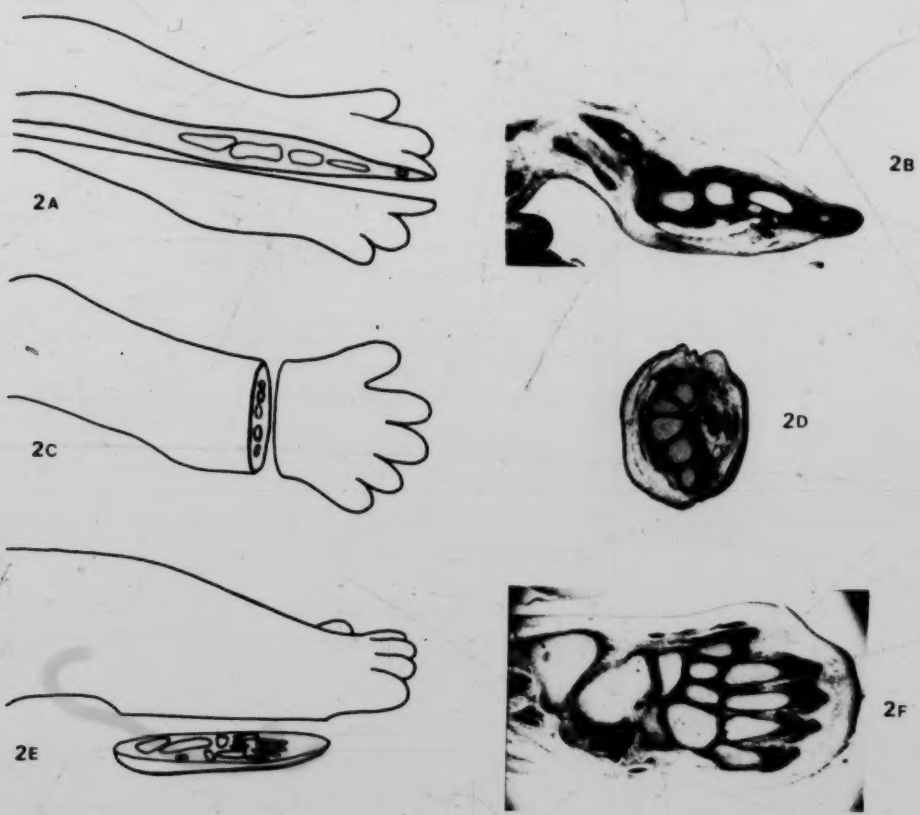
The ability to discern internal structures varies with the plane of section. Verbout (1985) considered the most accurate interpretation of the internal elements to be based on analysis of sections from all three planes. This enables the observations from one plane to be crosschecked against those from the two other planes. Therefore, it was fortunate that the specimens considered suitable for this study

represented the three sectional planes.

Fig 1. Comparison of the embryonic position (A and B) and the standard anatomical position (C).

Fig 2. Sectional planes through the embryonic foot.
A) sagittal plane as in embryos XXa and XXIIb
B) sagittal section from embryo XXa
C) coronal plane as in embryos XXb and XXI
D) coronal section from embryo XXI
E) horizontal plane as in embryos XXIIa and XXIII
F) horizontal section from embryo XXIIa


1A
1B
1C


2A
2B
2C
2D
2E
2F

B. METHODS

To reveal the spatial relationships of the musculoskeletal structures during development, three-dimensional reconstructions were developed from the serial sections, following the recommendation of O'Rahilly (1972). A preliminary review of the literature revealed that numerous methods of reconstruction have been developed for microanatomical studies. Stereoscopic reconstruction and serial section cinematography were discarded from the outset due to numerous disadvantages outlined by Gaunt and Gaunt (1978). Graphical reconstruction, although simpler to produce than solid reconstructions, would ultimately be more time-consuming; since each two-dimensional drawing can represent only one view of the reconstructed model, each additional view would require the contours to be redrawn. Moreover, it would be very difficult to achieve mathematically correct proportions of the perceived dimension of depth. The most efficient and effective method of reconstruction might have been computergraphics had the facilities and software been available.

Wax-Plate Reconstruction

The small number of researchers employing reconstructions in their examination of embryonic development of the foot, applied the wax-plate method devised by Born (1876, cited in Bardeen, 1901). This method was selected initially for this study but it was readily

apparent that it would not be possible to examine both the skeletal and muscular tissues in the same reconstruction; skeletal structures would be almost entirely obscured in the wax model by the overlying musculotendinous structures. It was resolved to reconstruct only the skeletal elements in the form of a wax model and to examine the relationship of muscular elements directly from the serial sections.

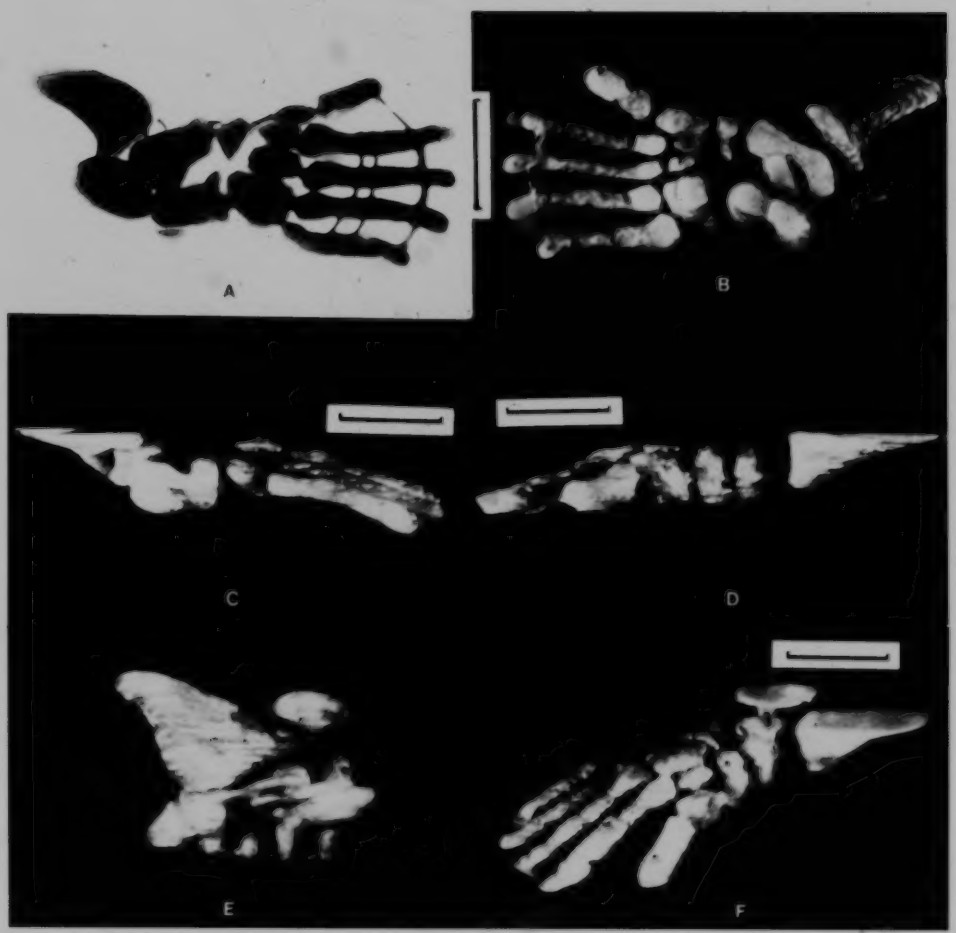
Embryo XXIIa was selected for this initial model because the right foot had been sectioned in the horizontal plane. Tracings of skeletal elements in this plane were considered easier to align using the method of best fit than serial tracings in either the coronal or sagittal planes (see Fig 2).

Briefly, the generation of the wax reconstruction involved the stacking of a series of wax-plate contours traced from the projected image of each serial section. A detailed account of the procedure is contained in Appendix A.

From the wax model, the shape, orientation and relative positions of the chondrified skeletal elements of the foot could be viewed from any angle (Fig 3). However, the intricate wire bridges that were required to retain the shape and spatial relations of the bones made construction difficult (Fig 3a). As a result, the wax-plate method was not considered well-suited to the study of disconnected structures such as the individual skeletal elements of the foot. This technique was abandoned in favour of

Fig 3. Wax-plate reconstruction of embryo XXIIa.

A) dorsal view demonstrating some of the internal wire bridges required to retain the relationships of the bones
B) plantar view
C) fibular view
D) tibial view
E) posterior view
F) oblique dorsotibial view
Calibration Bar = 1mm


A
B
C
D
E
F

reconstruction using transparencies.

Transparency Reconstructions

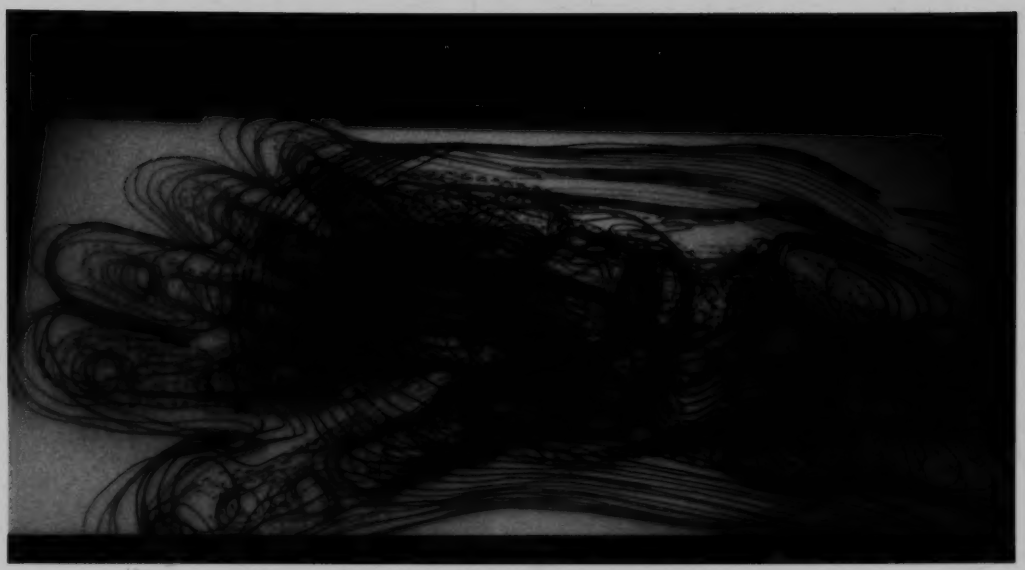
The transparency reconstruction method used in this study was adapted from Gaunt and Gaunt (1978) and is fully described in Appendix B. Appendix C outlines the various other transparency methods that were tried but found to be unsatisfactory. Briefly, the procedure that was finally adopted involved projecting each serial section with a microprojector and tracing the contours of the relevant structures directly onto transparent acetate sheets. Coloured pens for overhead transparencies were used and the outlines of different tissues were colour-coded. A separate tracing was made for each section in the series after which the tracings were aligned using the method of best fit. Then, each acetate sheet was mounted on an individual frame, the thickness of which was proportionate to the distance between the enlarged sections. When the mounted tracings were stacked in their correct, aligned sequence, the frames served as spacers between the tracings to establish the correct perspective of depth in the model.

When viewed by transillumination (i.e. with light shining through from below), the transparent nature of the reconstruction permitted simultaneous visualization of all the internal structures in the limb. As the acetate sheets had been separated with spacers, it was possible to examine the internal elements from a wide range of oblique views

(Fig 4). This feature greatly enhanced the informative value of the transparency reconstructions. However, it was not possible to observe the reconstructed image from views that were perpendicular to the plane of section. Therefore, to visualize the internal arrangement from all angles, it was necessary to have at least one transparency model for each of the three planes of section.

In total, four transparency reconstructions were made, one for each of the last four stages of embryonic development (see Table 1). These models provided three different views of the embryonic foot because they were developed from specimens that had been sectioned in three different sectional planes: one each in the sagittal (embryo XXa) and coronal (embryo XXI) planes and two in the horizontal plane (embryos XXIIa and XXIII) (Figs 5 - 8). To compare the two reconstruction techniques, embryo XXIIa was reconstructed using both the wax-plate and transparency methods (see Figs 3 and 4).

As table 1 indicates, not every section in the series was mounted for embryo XXIII, nor do the records indicate the interval between the mounted sections. Therefore, it was necessary to estimate the interval by trying different widths of spacers between the acetate tracings and using the reconstruction of embryo XXIIa, also sectioned in the horizontal plane, as an indication of the dimension of depth. It was concluded that only every fourth section of the series had been mounted.



A

B

Fig 4. Transparency reconstruction of embryo XXIIa.

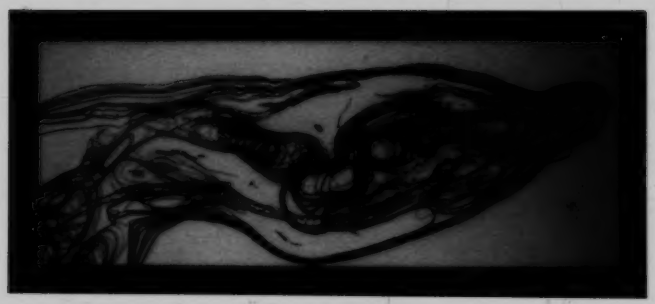
A) dorsotibial view
B) dorsofibular view

Figs 5 - 8. Photographs of the transparency reconstruction all reproduced to the same magnification in order to show relative size.

black: outline of limb and definitive cartilage;
green: condensed mesenchyme, perichondrium, ligaments;
blue: muscle;
brown: tendon;
purple: nerve;
red: blood vessels

Fig 5. A) Transparency reconstruction of embryo XXa (fibular view).
B) Region of embryo XXa included in the reconstruction.

Fig 6. A) Transparency reconstruction of embryo XXI (posterior view).
B) Region of embryo XXI included in the reconstruction.



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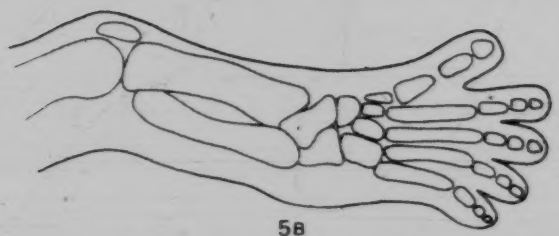

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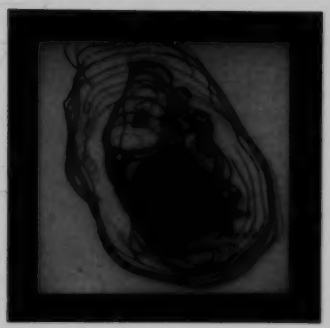

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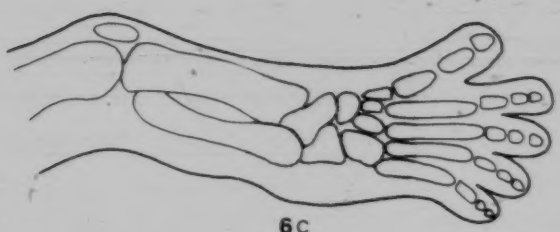
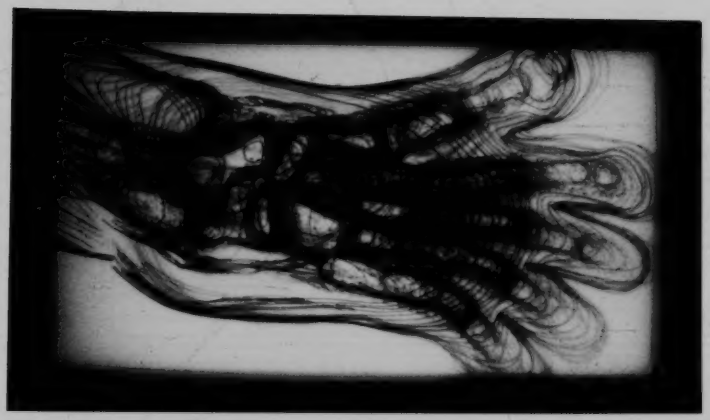


6C

Fig 7. A) Transparency reconstruction of embryo XXIIa (dorsal view).
B) Region of embryo XXIIa included in the reconstruction.

Fig 8. A) Transparency reconstruction of embryo XXIII (dorsal view).
B) Region of embryo XXIII included in the reconstruction.



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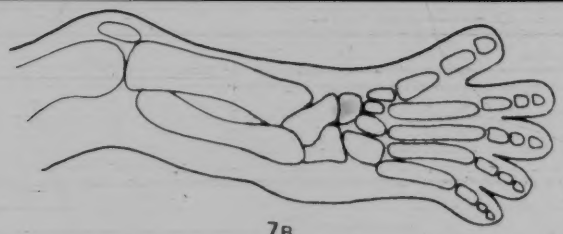

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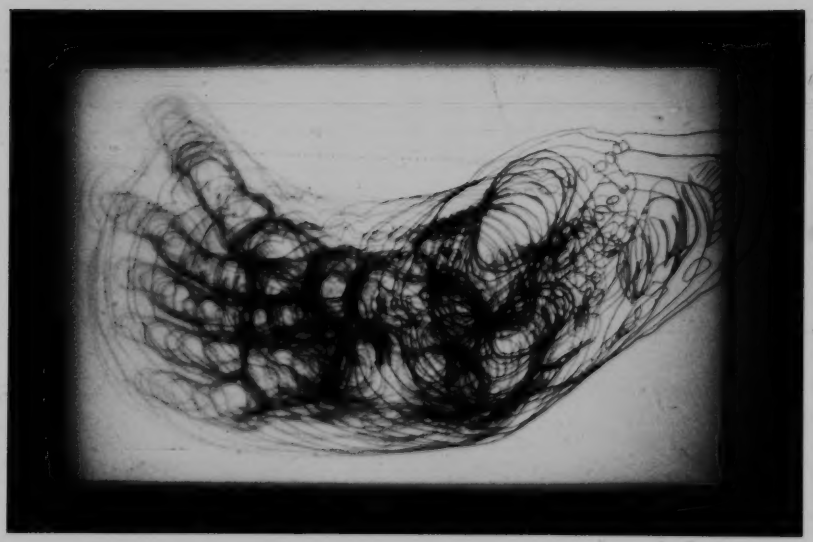

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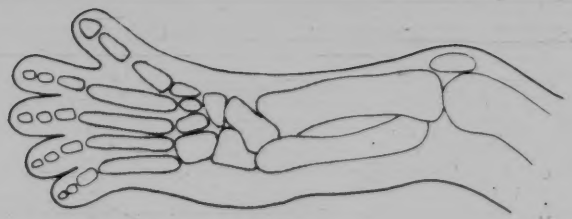


8B

To assess distortion of the reconstructed image caused by refraction of light passing through the stack of mounted acetate tracings, a narrow beam of light was shone through the transparency models of embryo XXI. No bending of the light beam was observed as it passed through the acetate sheets, irrespective of the angle of incidence. It was concluded that there was no apparent distortion of the image caused by refraction of light.

The internal structures of the reconstructed embryonic limbs were studied by setting each transparency model on a light box which provided the transillumination necessary to view through the stack of framed acetate tracings. For the first transparency model assembled (embryo XXa), all internal structures were examined (i.e. the musculoskeletal and neurovascular structures). The neurovascular elements were observed as basically similar to the adult situation, except for the absence of the deep veins. Therefore, it was resolved to focus all subsequent attention only on the musculoskeletal structures. Nonetheless, the contours of the neurovascular structures were included in the other three models because they served as auxiliary points of reference to facilitate the process of aligning the tracings (see Fig 5 - 8). The features described from the transparency models included:

1. the postural features
2. the size, shape, orientation and relationships of the skeletal elements and the associated ligaments

3. the course and distal attachments of the extrinsic tendons
4. the arrangement and attachments of the intrinsic muscles.

Observations regarding the progressive development of the joints were not made because this aspect of embryonic development has already been extensively documented elsewhere (Haines, 1947; Gardner *et al.*, 1959; Drachman, 1969).

In addition to the morphological observations, quantitative measurements of the skeletal elements were made (Fig 9). Angles between the skeletal elements were measured with a goniometer while dimensions were measured with calipers (Fig 10). These measurements were taken from the transparency models, with consideration of the magnification. Alternatively, they were calculated by counting the number of sections that contained the structure being measured. The wax model was not considered appropriate for these measurements because the dimensions had been slightly altered in the process of smoothing out the stepped appearance of the skeletal elements.

To determine the dimensions and angles from the contours that were situated obliquely through the transparency model, the method of measuring within the reflected image was used (see Fig 11).

The error of measurement was assessed by selecting at random five of the 13 items from figure 11 and measuring

Fig 9. Dimensions and angles of the embryonic skeletal elements, measured from the transparency reconstructions.

A) length of the first metatarsal (M1) through its central long axis

B) length of second metatarsal (M2) through its central long axis

C) length of third metatarsal (M3) through its central long axis

D) length of the calcaneus through its central long axis

E) length of the talus through its central long axis

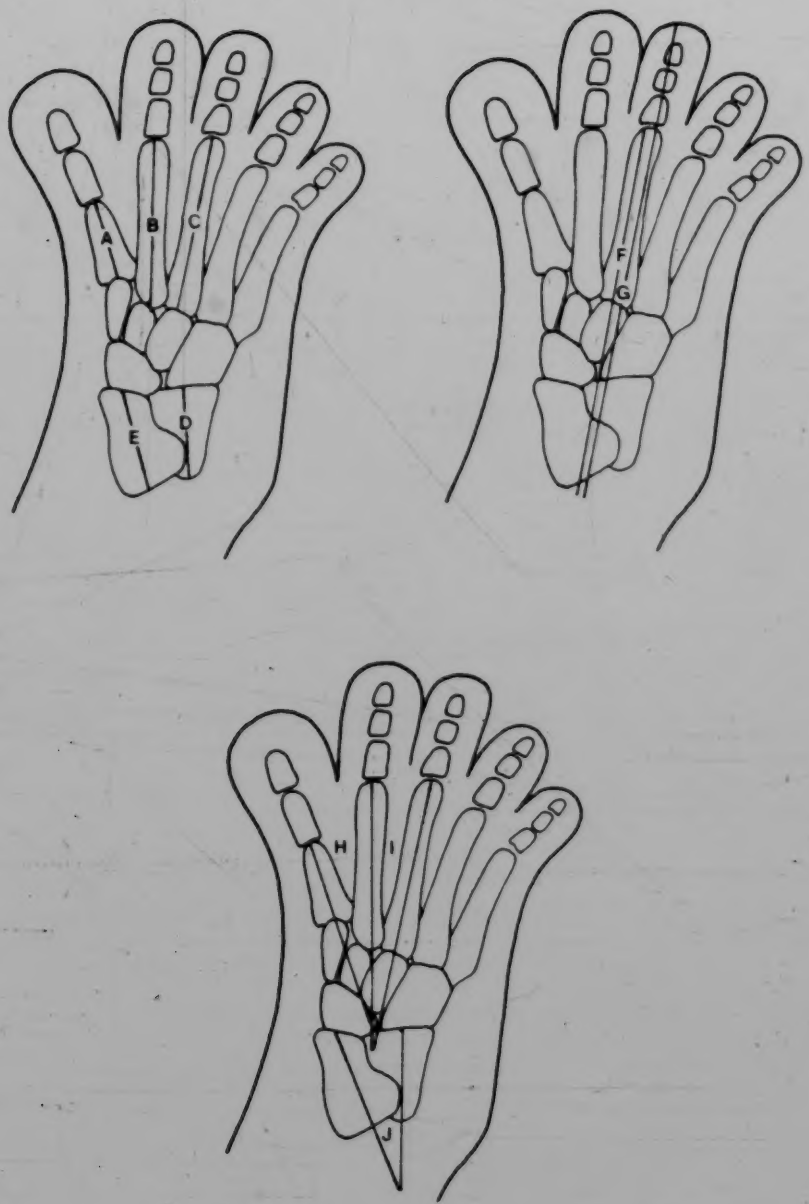
F) total length of the tarsal and metatarsal elements i.e. from the most posterior projection of the tarsal bones to the most distal projection of the metatarsals

G) total foot length i.e. from the most proximal projection of the tarsal bones to the most distal projection of the toes

H) angle between the central long axes of the shafts of M1 and M2

I) angle between the central long axes of the shafts of M2 and M3

J) angle between the central long axes of the talus and the calcaneus i.e. talocalcaneal angle in the AP view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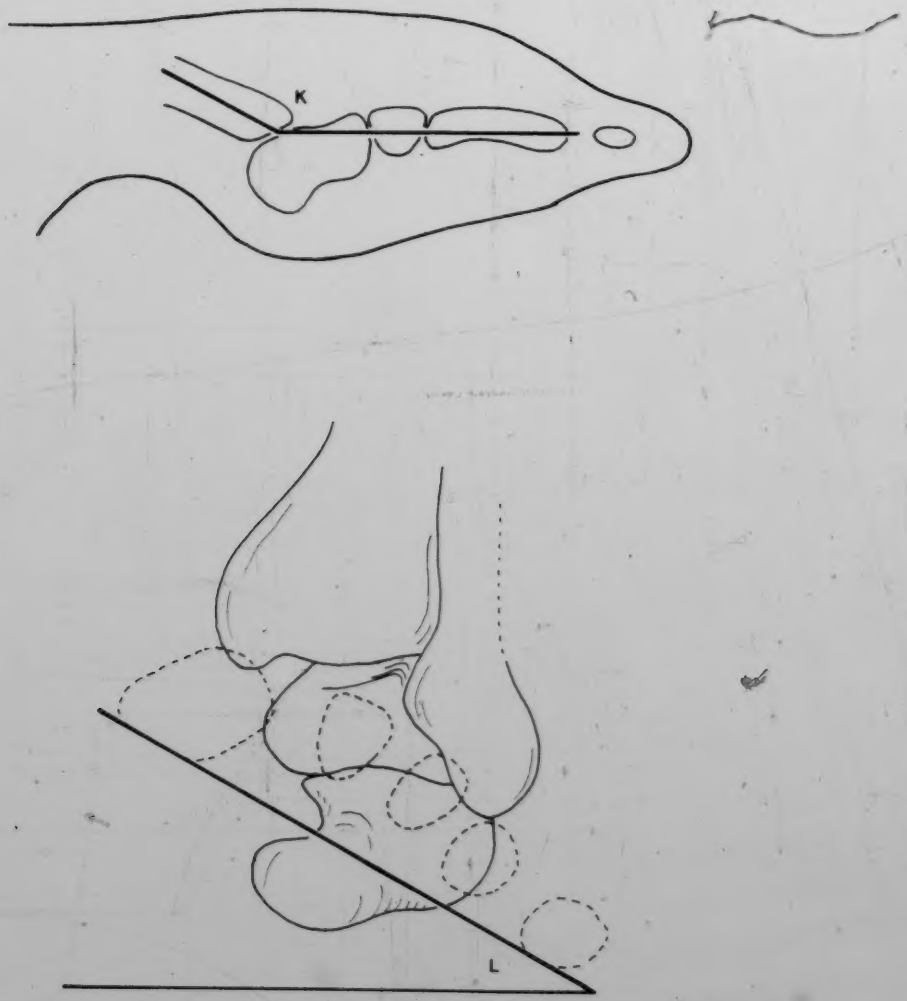


Fig 9. continued
K) angle of plantar flexion at the ankle measured from the fibular side of the limb = K - 90°.
The axis of the goniometer is placed on the fibular malleolus; one arm of the goniometer is set on the central long axis of the lower 2/3 of the fibula while the other arm intersects the head of the fifth metatarsal.

L) angle between the theoretical weight-bearing plane of the foot and the line intersecting the bases of the first and fifth metatarsals (i.e. the amount of inversion of the forefoot)

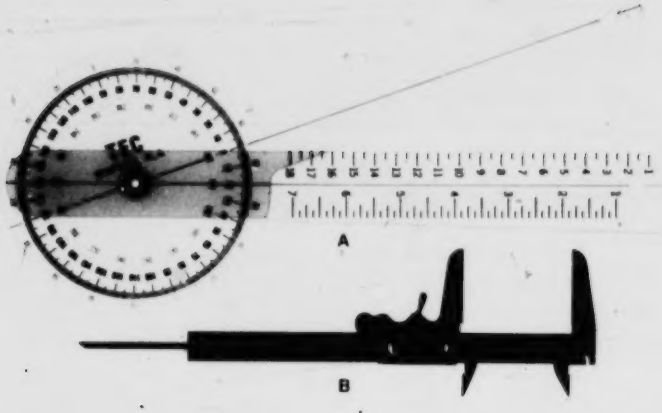


Fig 10. Tools to measure the embryonic skeletal elements in the transparency reconstructions.

A) Goniometer
B) Calipers.

Fig 11. Procedures used to measure within the reflected image of the transparency reconstructions.

A) The light box (LB)is set on end so that its illuminated surface is vertical with the plate of reflective glass (G). The transparency model of embryo XXIIa is set on its side against the light box.

B) The goniometer is held behind the glass plate.

C) The measuring device is viewed through the plate of glass and can be oriented such that it appears to be situated within the reflected image and in the same plane of the structure(s) being measured. The image appears to be out of focus in this photograph because it is being formed on both the front and back surfaces of the plate of glass. This however did not impede the measuring process or distort the measurements.

A
M
G
LB
B
G
C

them on ten separate occasions. From these scores, the mean, standard deviation and coefficient of variation were calculated for each test items (see Table 2). The results of this experiment indicated that the coefficient of variation never exceeded 5%, indicating a high degree of reliability in the methods used to make the measurements.

For the purpose of presenting the results in this thesis, it was necessary to reproduce the three-dimensional transparency models in a two-dimensional format. However, it is readily apparent from figures 4 through 8 that the transparency models did not lend themselves to photographic reproduction because the numerous overlying contours created a visually confusing image. A more comprehensible image was produced by tracing the relevant structures from photographs onto paper. These illustrations omitted the superfluous contours which in the photographs had obscured the essential aspects of the models (Fig 12).

After the models had been studied, the serial sections of the four embryos were examined by light microscopy to discern the details not readily apparent in the enlarged projected image. The information obtained from these four embryos was then supplemented by studying the serial sections of two additional embryos (XXb and XXIIb) using light microscopy alone. Experience gained from constructing and examining the models made it possible to appreciate the spatial relationships of the internal structures directly from the serial sections. Representative fields were

TABLE 2. MEAN, SD AND COEFFICIENT OF VARIATION OF SELECTED MEASUREMENTS OF EMBRYONIC SKELETAL ELEMENTS

Measurement	Embryo #	Mean (N=10)	Standard Deviation	Coefficient of Variation
Length of MT1 (A)	XXIIa	.65 mm	.01 mm	1.47
	XXIII	.87 mm	.01 mm	1.49
Length of MT2 (B)	XXIIa	1.29 mm	.01 mm	.94
	XXIII	1.26 mm	.01 mm	1.13
Angle Between MT1 & MT2 (I)	XXIIa	19.45°	.65°	3.34
	XXIII	20.55°	.69°	3.60
Angle Between MT2 & MT3 (J)	XXIIa	9.00°	.32°	3.55
	XXIII	10.60°	.44°	4.15
Angle of Ankle Dorsiflexion (K)	XXa	27.70°	1.03°	3.73

Numbers in brackets refer to items in Fig 9

Coefficient of Variation = SD/Mean x 100 (Cameron, 1984)

Fig 12. Illustration (A) of the Skeletal Elements of Embryo XXI produced from a Black and White Print (B) of the Transparency Reconstruction.

photographed onto Kodak panatomic X (ASA 32) film using a Leitz 45MPS photomicroscope and then enlarged prints were made on Ilford Ilfospeed multigrade II (MG.1M) photographic paper. The complete series of sections for each of the six embryo are contained in Appendix D.

C. ADULT SPECIMEN

For reference purposes, the end point of the developmental continuum was considered to be the adult situation. Consequently, an intact, adult, right leg and foot was obtained from the cadaveric material available in the Department of Anatomy. The specimen was selected at random with the precondition that it showed no obvious external abnormalities. Unfortunately, the sex and age were not known.

The limb was carefully dissected to demonstrate the morphology and relationships of the musculoskeletal structures (Fig 13). During this process, an extensive series of colour slides was taken using Kodak Ektachrome 160 tungsten film, employing either a Canon AE-1 camera with a 50mm macro lens or a Praktica LTL camera with a Zeiss 50mm lens. These slides were subsequently reproduced as colour prints.

In the course of the dissection, an insignificant bony spur projecting from the lower posterior aspect of the tibia was discovered. However, since there was no evidence of deformity of the structures in the foot, the observations recorded from this foot were considered to be representative of the typical adult situation.

Fig 13. Partially dissected adult right lower limb (lateral view).

Summary of Materials and Methods

The materials used in the study included six serially sectioned human embryos and one adult leg and foot. The methodology had five components:

1. the wax-plate reconstruction of embryo XXIIa
2. the transparency reconstructions of embryos XXa, XXIIa, XXIII and XXI (in that order)
3. the examination of serial sections of these four embryos by light microscopy
4. the examination of serial sections of two additional embryos (XXb and XXIIb)
5. the detailed dissection of an adult leg and foot

D. DEFINITION OF TERMS

Some of the terminology used to describe the findings require explanation. By convention, the terms "medial" and "lateral" denote the inner and outer aspects of the lower limb respectively. However, these labels are based upon the standard anatomical position and are not appropriate for describing the embryonic situation where the orientation of the lower limb is very different (see Fig 1). Instead, as advocated by Jones (1949) and Cihak (1972), the terms "tibial" and "fibular" have been used to represent the inner and outer sides respectively of the lower limb (Fig 14).

Using the definition proposed by Basmajian (1981), the three regions of the foot skeleton are as follows (Fig 15). The "hindfoot" refers to the talus and calcaneus as well as the distal ends of the tibia and fibula. The navicular, cuboid and the three cuneiform bones comprise the "midfoot". Within the midfoot, the tibial-sided cuneiform is identified as the first cuneiform. The fibular-sided cuneiform is the third cuneiform and the intervening bone is the second cuneiform. The "forefoot" includes the metatarsal and phalangeal bones.

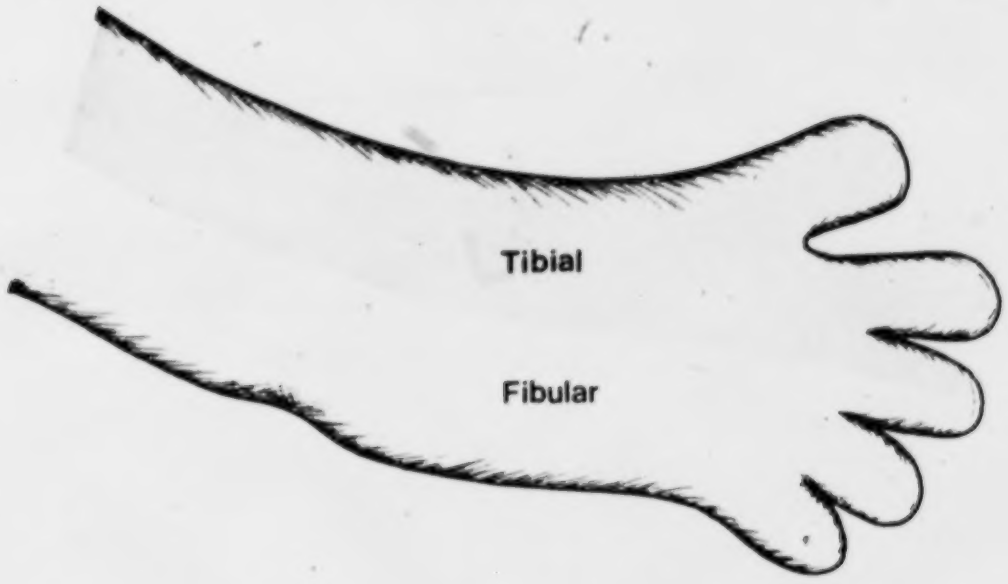


Fig 14. The tibial (shaded) and fibular sides of the lower limb (based on Jones, 1949).

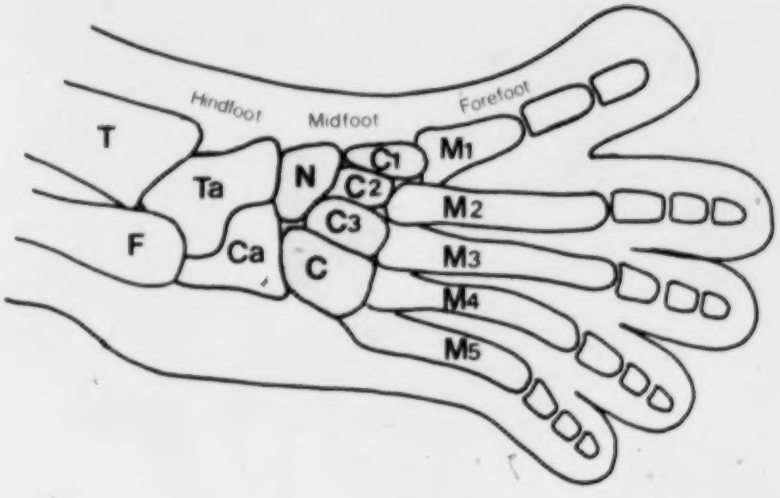


Fig 15. The three subdivisions of the foot (applying to both the embryonic and adult conditions).

IV. RESULTS

This section reports the findings from the six embryos selected from the Shaner Collection, comparing certain features to those observed in an adult lower limb. These results, based on the observations from serial sections and three-dimensional reconstructions, focus on the postures and the musculoskeletal structures of the foot during the last four stages of embryonic development (stages 20 to 23).

The findings from the embryonic specimens have been presented in the following sequence:

1. postures of the foot
2. skeletal elements
3. extrinsic muscles
4. intrinsic muscles

Each of these aspects will be dealt with in turn, identifying developmental trends over the four represented embryonic stages, noting any differences between the specimens and comparing them to the adult situation.

A. THE POSTURES OF THE EMBRYONIC FOOT

Prior to sectioning, the external appearance of four of the six embryos was recorded. Unfortunately, these illustrations provided only a general indication of the posture of the lower limb (Fig 16). As a result, the observations concerning the postural features were interpreted primarily from the wax and transparency reconstructions. This information was supplemented by studying the serial sections of the two specimens that had not been reconstructed.

The postural changes observed between stages 20 and 23 are depicted in figure 17. The most striking postural feature was the marked lateral rotation of the lower limb as a whole. At stage 20, the limb was laterally rotated approximately 90 degrees from the anatomical position with the tibial border of the foot and leg directed cranially and the fibular border directed caudally (Fig 17A). As a result, the extensor (future anterior) surface of the limb was oriented laterally and the flexor (future posterior) surface faced medially. The sole of the foot at stages 20 and 21 had a cranio-medial orientation and was facing toward the umbilical cord. This indicated that the foot was inverted relative to the leg. A progressive medial rotation of the entire limb (towards the anatomical position) was observed over the next three stages. The lateral orientation of the knee, apparent at stage 20, had changed to a more cranio-lateral orientation by stage 23. The sole was now

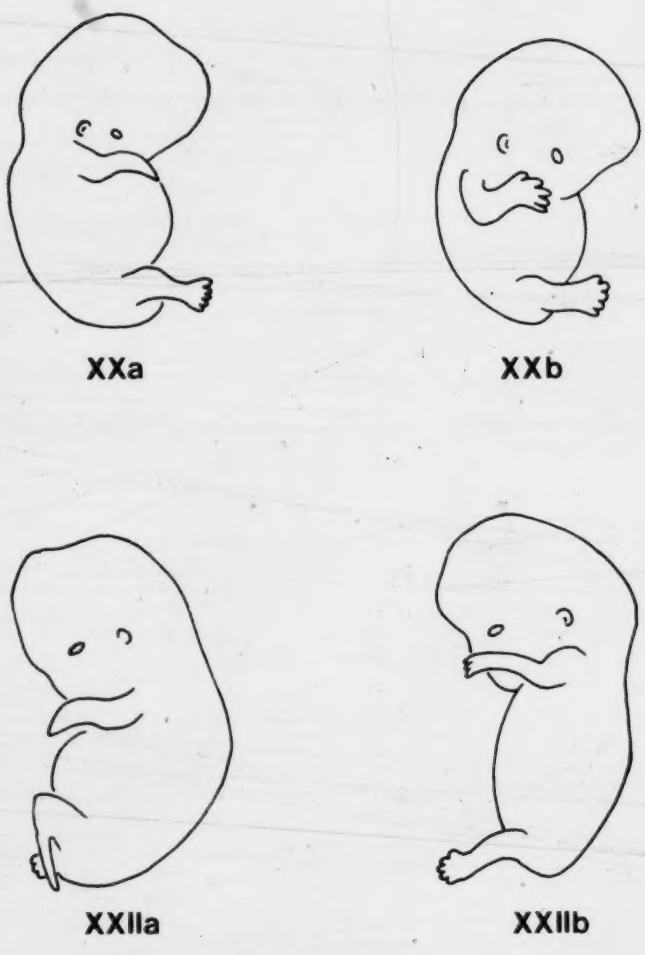


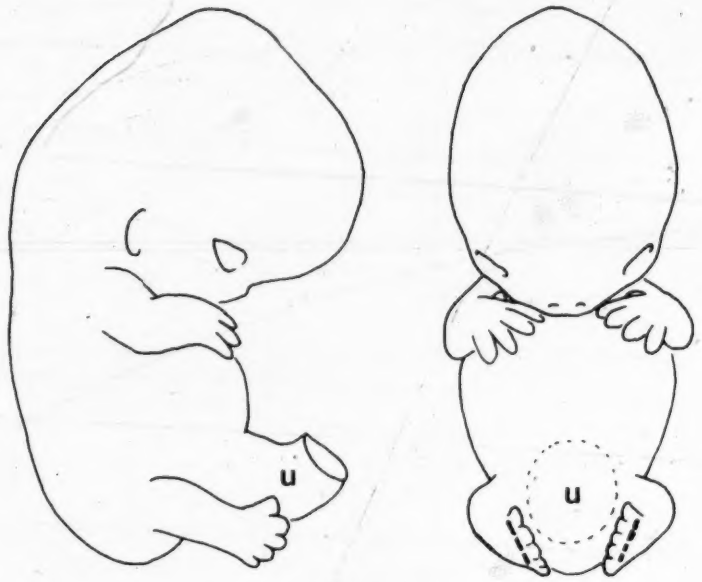
Fig 16. External appearance of the embryos recorded prior to sectioning.

The illustrations of embryos XXa, XXIIa and XXIIb were traced from the original line drawings. The illustration of embryo XXb was traced from the original photograph. (The external appearance of embryos XXI and XXIII was not recorded prior to sectioning.)

Fig 17. Postural changes of the embryonic lower limbs during stages 20 through 23.

A) Stage 20, the lower limb as a whole is laterally rotated approximately 90° from the anatomical position with the extensor (future anterior) surface facing laterally and the flexor (future posterior) surface facing medially. The sole of the foot is facing the umbilical cord (u), having a cranio-medial orientation.

B) At stage 23, representing the end of the embryonic period, the knee has a cranio-lateral orientation, the sole faces medially and the great toe is directed cranially. These changes are attributed to medial rotation of the lower limb as a whole.



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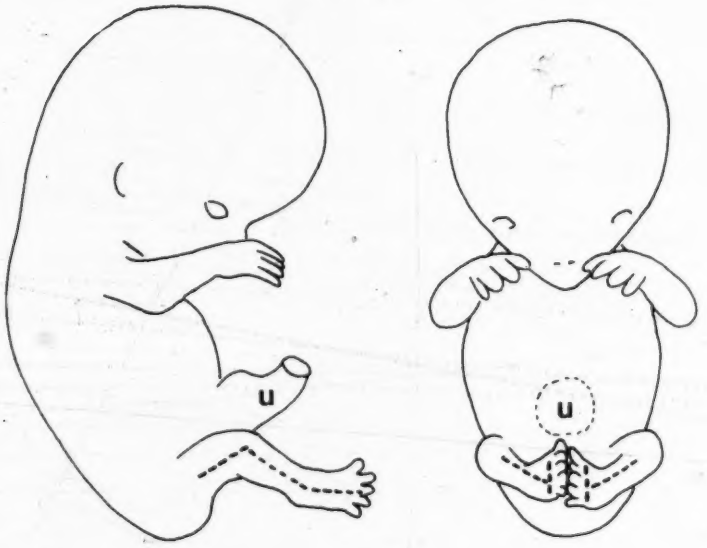


B

directed medially and the great toe was oriented cranially (Fig 17B).

Another difference between the embryonic foot posture and the adult anatomical position was the marked plantar flexion at the ankle which, although apparent at all stages, was readily visualized in the sagittally-sectioned specimens (Fig 18A). The model of embryo XXa was the most extensive reconstruction in that it provided a view of the fibular side of the limb which extended proximally to include the condyles of the femur (see Fig 5). As a result, the angle at the ankle could be measured and was found to be 62° of plantar flexion (see Fig 9K).

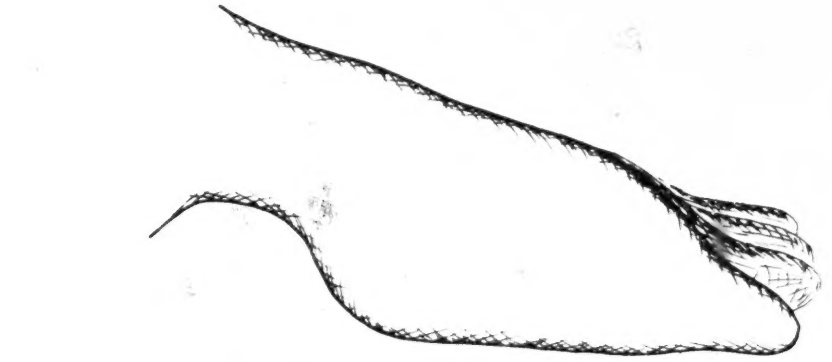
The reconstructions of the horizontally-sectioned specimens (XXIIa and XXIII) demonstrated that the foot as a whole was adducted toward the tibia (Fig 18B and C). Figure 18B also demonstrates that the external form of the foot of embryo XXIIa was strikingly similar to a postnatal hand. This was due to the general abduction of the toes, especially, the first. In addition, the "digital formula" (i.e. the relative length of the toes) was the same as the standard digital formula for the fingers (i.e. 3>2>4>5>1) and distinctly different from the typical formula for the adult foot (i.e. 1>2>3>4>5) (Jones, 1949). It was not possible to accurately determine the digital formula for the other specimens, although dominance of the second and third toes along with a relatively short first toe was also evident in embryos XXa, XXI and XXIIb.

Fig 18. External appearance of the embryonic lower limb (drawn from the transparency reconstructions).

A) Embryo **XX**a.
View of fibular side of the right leg and foot demonstrating marked plantar flexion at the ankle.
(5 - fifth digit)

B) Embryo **XXII**a.
Dorsal view of the right leg and foot demonstrating adduction of the foot toward the tibia.
(1 - first digit)

C) Embryo **XXIII**.
Dorsal view of left leg and foot demonstrating marked adduction of the forefoot toward the tibia.
Consequently, the fibular border is convex and the tibial border is concave.



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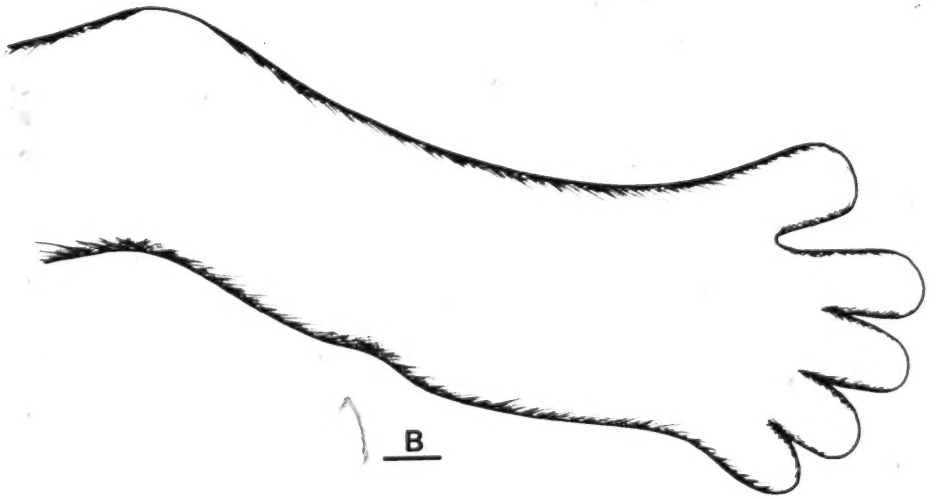

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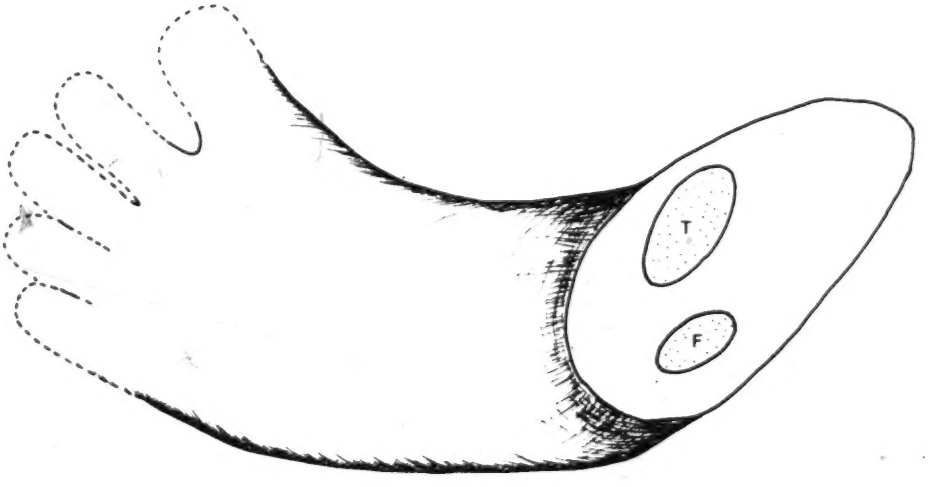


C

In **summary**, the postural features of the lower limbs of these embryos included:

1. lateral rotation of the entire limb
2. plantar flexion at the ankle
3. adduction of the foot toward the tibia.
4. marked divergence of the first toe at stage 22
5. marked forefoot adduction at stage 23

During the subsequent process of studying the musculoskeletal structures of the foot, it became apparent that understanding the posture of the embryonic foot as it compared to the anatomical position was essential to the correct interpretation of the arrangement of these internal structures.

B. THE SKELETAL ELEMENTS

A progressive maturation of the cartilaginous skeletal elements of the leg and foot was observed over stages 20 through 23 (Fig 19). Perhaps the most significant finding was that the phalanges chondrified later than the other elements of the foot, progressing in a proximodistal sequence in each toe. At stage 20, only the proximal phalanges were chondrified, whereas the middle and distal phalanges were represented by unsegmented condensed mesenchyme (Fig 19A). During stages 21 and 22, both the proximal and second phalanges were chondrified (Fig 19C). The distal phalanges of the outer four toes were not chondrified until stage 23. Presumably, the long flexor and extensor tendons would not be anchored distally until the middle and distal phalanges were chondrified.

No evidence of marrow formation was found in any of the specimens; all of the skeletal elements were either mesenchymal or cartilaginous. Therefore, using the onset of ossification as the criterion to mark the transition from the embryonic to the fetal period (Streeter, 1951), all six specimens were considered to be embryos. However, one of the sections through the femur of embryo XXIII revealed the penetration of a periosteal bud, indicating that ossification was imminent (Fig 19D).

Accessory ossicles were observed in embryos XXI, XXIIb and XXIII (Fig 20). The most striking of these was the chondrified ossicle attached to the posterior edge of the

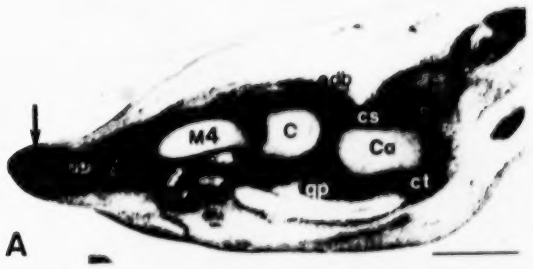
Fig 19. Photomicrographs demonstrating progressive maturation of the cartilaginous skeletal elements.

A) Embryo XXa.
Sagittal section through lower part of the right leg and foot viewed from the tibial side, demonstrating the precartilaginous nature of the calcaneal tuberosity (ct) and the anterior process of the calcaneus (ap). In the toes, only the proximal phalanx (pp) has begun to chondrify at stage 20. The middle and distal phalanges are represented by unsegmented condensed mesenchyme (arrow). Also shown is the proximal attachment of quadratus plantae (qp); and the calcaneal sulcus (cs) with the proximal attachment of extensor digitorum brevis (edb).

B) Embryo XXIIb.
Sagittal through the right foot, viewed from the tibial side, to show that chondrification is more advanced than at stage 20. Note: the anterior process and tuberosity of the calcaneus are now chondrified; the calcaneal sulcus; the proximal attachments of extensor digitorum brevis and quadratus plantae. Unfortunately, the toes are incomplete in the serial sections of the specimen. Consequently, they cannot be observed beyond the proximal phalanx.

C) Embryo XXIIa.
Horizontal section through the right foot viewed from above demonstrating the chondrified proximal (pp) and middle phalanx (mp) and the blastemal distal phalanx in the third digit (arrow).

D) Embryo XXIII.
Oblique section through the left femur (Fe) demonstrating the penetration of a periosteal bud (arrow), indicating that ossification is imminent. (Calibration bar = .05mm in **D**)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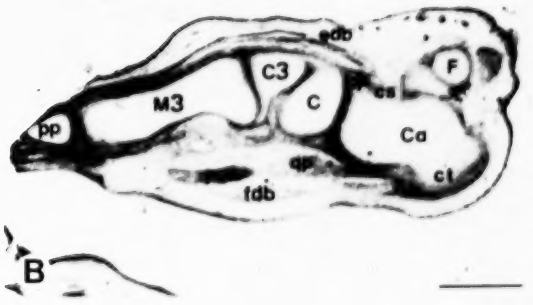
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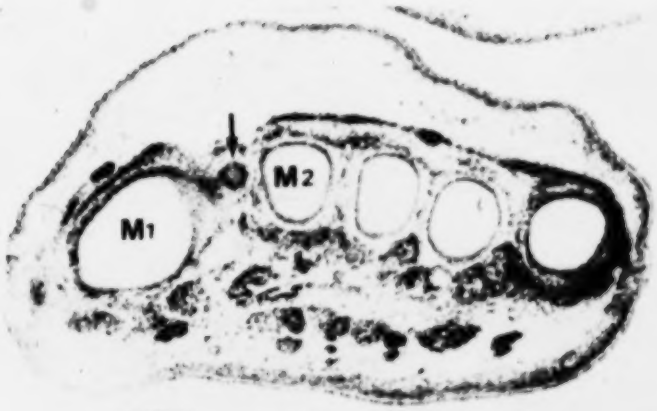
Fig 20. Photomicrographs of embryonic accessory ossicles.

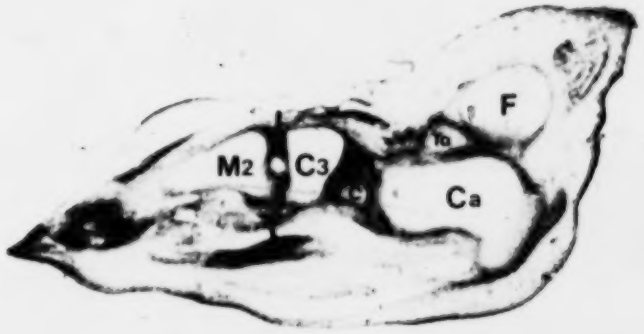
A) Embryo XXI.
Coronal section through the right foot viewed from behind. There appears to be a slightly chondrified accessory ossicle (arrow) located between the proximal portion of the first and second metatarsals (M1 and M2).

B) Embryo XXIIb.
Sagittal section through the right foot viewed from the tibial side. There appears to be a chondrified accessory ossicle (arrow) situated in the interzone between the fibular side of the base of the second metatarsal (M2) and the tibial half of the third cuneiform (C3).

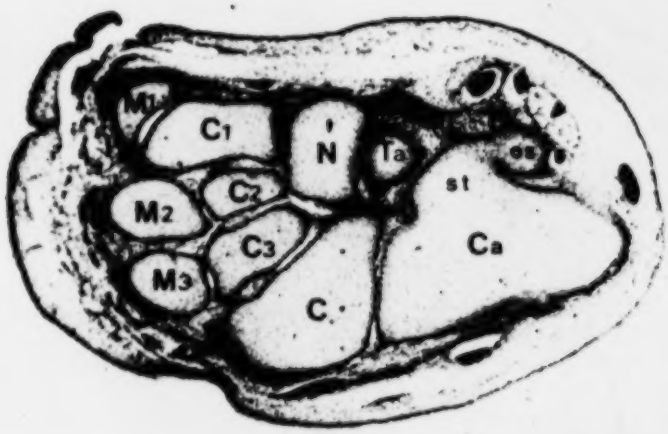
C) Embryo XXIII.
Horizontal section through the left foot viewed from above. An accessory ossicle (os) is fused to the posterior edge of the sustentaculum tali (st).



A



B



C

sustentaculum tali in embryo XXIII (Fig 20C).

When the size, shape and relationships of the skeletal elements in the embryonic specimens were compared to the adult foot, numerous differences were observed. One of the most striking contrasts was the configuration of the longitudinal arches (Fig 21). Whereas the adult foot demonstrated a well-developed arch along the tibial border of the foot (i.e. the medial longitudinal arch), this border was completely flat in the wax model of embryo XXIIa. It was surprizing therefore to observe that in the same model, as well as the sagittal sections of embryos XXa and XXIIb (Fig 21E) the fibular side of the foot was arched similar to the adult lateral longitudinal arch. The observation of the embryonic fibular longitudinal arch in the absence of a tibial longitudinal arch was a sharp contrast to the adult foot where the tibial border was actually arched more than the fibular side.

Transverse arching of the skeletal elements in the embryonic feet was quite similar to the adult configuration, although not as pronounced (Fig 22). Whereas the bases of the metatarsals were separated from each other at stage 20, by stage 23 a close-packed fitting of the bases, similar to the adult condition, was apparent. Unfortunately, it could not be determined whether a concommitant deepening of the transverse arch also occurred over this series because only stages 20 and 21 were represented by coronally-sectioned feet.

Fig 21. Comparison of the embryonic and adult longitudinal arches.

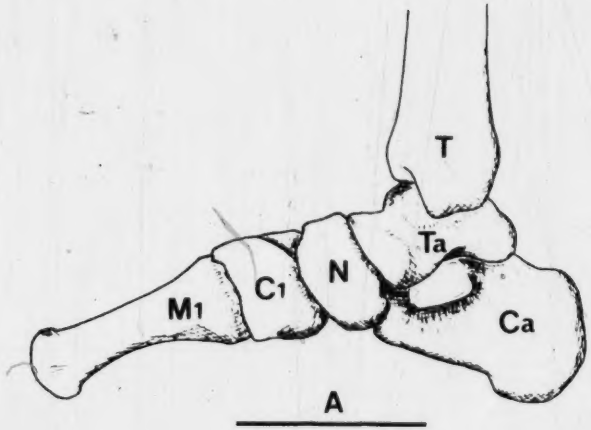
A) Adult, right foot.
The well-developed tibial (medial) longitudinal arch (redrawn from McMinn and Hutchings, 1977).

B) Embryo XXIIa, right foot.
The flat appearance of the tibial side of the embryonic foot, drawn from the wax model.

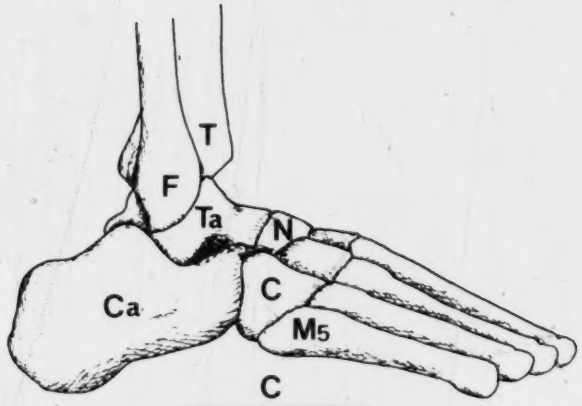
C) Adult, right foot.
The fibular (lateral) longitudinal arch (redrawn from McMinn and Hutchings, 1977).

D) Embryo XXIIa, right foot.
The arched configuration of the fibular side of the embryonic foot, drawn from the wax model.

E) Embryo XXIIb, right foot.
The tracing of the skeletal elements from a sagittal section viewed from the fibular side to emphasize the features contributing to the fibular arch: the plantar concavity of the outer four metatarsals (here M3), the wedge shape of the third cuneiform (C3) and the plantar projection of the calcaneal tuberosity (ct).



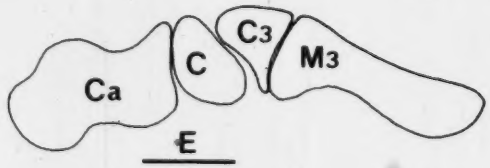
A



C

D

B



E

Fig 22. Comparison of the embryonic and adult transverse arch.

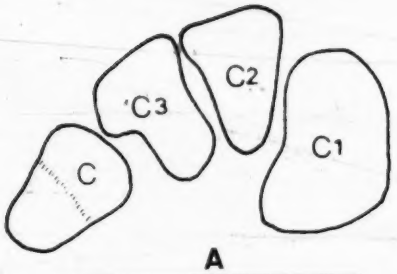
In both situations, the factors contributing to the transverse arch of the midfoot include the: wedge-shape of the cuneiform bones (C1, C2 and C3) and the bases of the metatarsals (M1, M2, M3, M4 and M5) as well as the more plantar plane of the first metatarsal (M1).

A) Adult, right foot.
The shape of the articular surfaces of the cuneiform bones and cuboid at the disarticulated tarsometataral joints, viewed from the front.

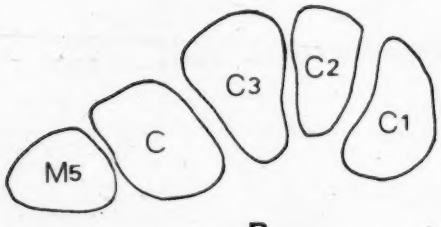
B) Embryo **XXI**, right foot.
The tracing of the skeletal elements from a coronal section viewed from the front. This section is located at approximately the same level as **A**), passing through the base of the fifth metatarsal, cuboid and the cuneiform bones. It demonstrates that the skeletal elements are arched similarly to the adult foot, although not quite as pronounced.

C) Embryo **XXI**, right foot.
The tracing of the skeletal elements from another coronal section viewed from the front, at a more distal plane than **B**), demonstrating the wedge-shape of the bases of the metatarsals.

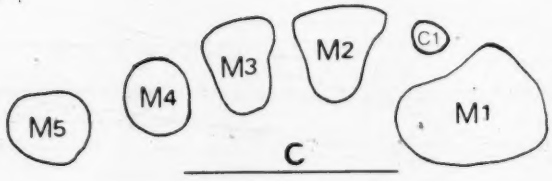
D) Embryo **XXII**a, right foot
The antero-inferior view of the skeletal elements of the foot, drawn from the wax model and demonstrating the transverse arch of the midfoot.


C3
C2
C1
C

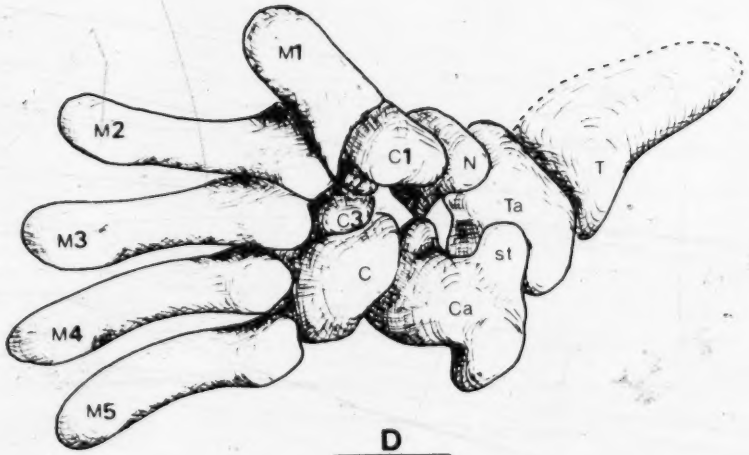
A


C3
C2
C1
C
M5

B


M3
M2
C1
M4
M1
M5

C


M1
M2
C1
N
T
Ta
C3
M3
st
C
Ca
M4
M5

D

The metatarsus demonstrated the most striking differences between the embryonic and adult specimens over the last four stages of embryonic development (see Table 3). These changes were readily visualized in the horizontally-sectioned embryos (Fig 23).

In the adult foot, the five metatarsal shafts were almost parallel to each other, the metatarsal heads articulated with each other, and the distal extent of the first and second metatarsals was almost equal (Fig 23A). In contrast, embryo XXIIa demonstrated a proportionately short, divergent first metatarsal along with general splaying of the outer four metatarsals (Fig 23B). The angle between the long axes of the second and third metatarsals measured 9°, whereas between the first and second metatarsals, 19° of abduction was measured (see Figs 9H and I).

The first metatarsal of XXIIa was only 50% as long as the second metatarsal compared to 83% in the adult foot. Due to this proportionately short first metatarsal, the first toe did not extend as far as any of the other four toes. This contrasted sharply to the adult situation where, in this specimen, the first toe extended the furthest (Fig 23). As a result of the fan-spread digits and the short, divergent first toe, the dorsal view of this reconstruction resembled more the outline of a hand than the outline of a foot (Figs 18B and 23B).

When the metatarsals of embryo XXIIa were compared to embryo XXIII, there were striking differences in their size,

TABLE 3. QUANTITATIVE MEASUREMENTS FROM EMBRYONIC SKELETAL ELEMENTS (see Fig 9)

Measurement	Embryo #	Value
Length of MT1 (A)	XXa	.35 mm*
	XXI	.45 mm*
	XXIIa	.65 mm
	XXIII	.87 mm
Length of MT 2 (B)	XXa	.60 mm*
	XXI	.78 mm*
	XXIIa	1.29 mm
	XXIII	1.26 mm
Length of MT3 (C)	XXa	.60 mm
	XXI	.78 mm
	XXIIa	1.21 mm
	XXIIb	1.10 mm*
Length of Calcaneus (D)	XXa	.72 mm
	XXI	.81 mm*
	XXIIa	.85 mm
	XXIIb	.90 mm*
	XXIII	1.16 mm
Length of Talus (E)	XXa	.72 mm
	XXI	.81 mm*
	XXIIa	.97 mm
	XXIIb	.85 mm*
	XXIII	1.10 mm
Length of Tarsus & Metatarsus (F)	XXa	1.90mm
	XXI	2.16 mm*
	XXIIa	2.65 mm
	XXIII	2.90 mm
Total Foot Length (G)	XXa	2.50 mm*
	XXIIa	3.90 mm
Angle Between MT1 & MT2 (H)	XXIIa	19.5°
	XXIII	21.6°
Angle Between MT2 & MT3 (I)	XXIIa	9.0°
	XXIII	10.6°
Angle Between Talus & Calcaneus (J)	XXIIa	20.0°
	XXIII	11.0°
Angle of Ankle Dorsiflexion (K)	XXa	27.7°
Angle of Forefoot Inversion (L)	XXI	35.0°

* indicates that the measurement is calculated from the number of serial sections

Fig 23. Size, shape and relationships of the embryonic skeletal elements (dorsal views, drawn from the transparency reconstructions) compared to the adult foot.

A) Adult, right foot.
B) Embryo **XXIIa**, right foot.
C) Embryo **XXIII**, left foot.

The toes have not been represented in embryo **XXIII** because they were damaged in the serial sections and could not be included in the transparency reconstruction.

The skeletal elements of the embryonic foot appear to be adducted toward the tibia, especially in embryo **XXIII** where adduction of the metatarsals is more pronounced.

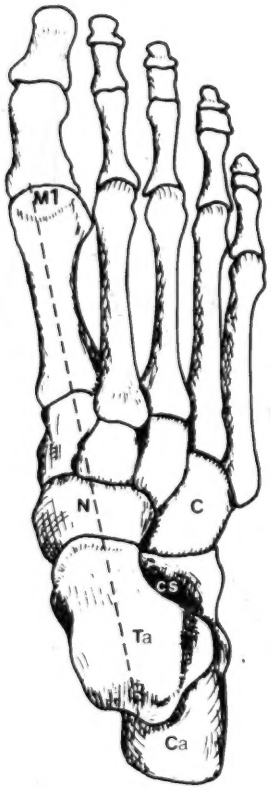
In the adult foot, the talus (Ta) is superimposed on the calcaneus (Ca) and the calcaneal sulcus (cs) is almost completely obscured. In contrast, the calcaneus (Ca) of the embryonic limbs appears to be situated on the fibular side of the talus (Ta) and the calcaneal sulcus is exposed.

Observe that in embryo **XXIIa**, the posterior part of the calcaneus is uncovered whereas in embryo **XXIII**, it is superimposed by the posterior process of the talus.

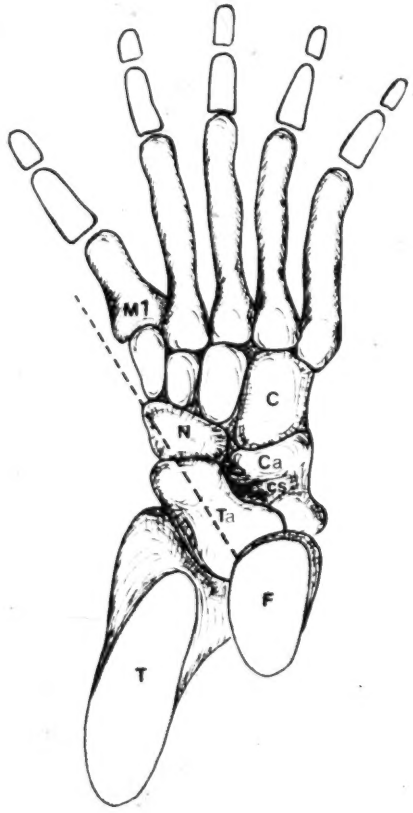
In embryo **XXIIa**, the long axis of the talus (broken line) passes to the tibial side of the first metatarsal whereas in embryo **XXIII**, it is passes between the first and second metatarsals. In the adult foot, this axis aligns with the first metatarsal (Huurman, 1978).

Both embryos demonstrate marked divergence of the first metatarsal (M1). Compared to both embryo **XXIII** and the adult, embryo **XXIIa** has an extremely short first metatarsal.

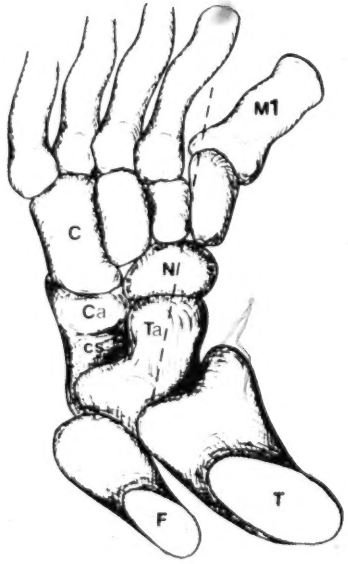
The outer four metatarsals of embryo **XXIIa** are somewhat fan-spread whereas in embryo **XXIII** they are concavely bowed towards the first metatarsal.



A



B



C

shape and orientation (Fig 23). Although there was no indication that the second metatarsal had grown in length from stage 22 to stage 23, the first metatarsal of embryo XXIII was actually 34% longer than in embryo XXIIa (see Table 3). As a result of this disproportionate growth, the first metatarsal of embryo XXIII was now 69% as long as the second, compared to 50% in embryo XXIIa.

Another unusual feature of the embryonic first metatarsal was the long, cartilaginous process at the attachment of the peroneus longus tendon; in the adult foot, no such process was observed (Fig 24). Whereas the facet for the first cuneiform demonstrated a flat surface in the adult foot, in embryos XXIIa and XXIII this surface was concave to accomodate the convex articular surface of the first cuneiform (Figs 23 and 24).

The orientation of the metatarsals had also changed from stages 22 to 23, due in part to increased adduction of the first metatarsal towards the tibia (Figs 23 and 24). This change was apparent from the shift of the long axis of the talus in a fibular direction in relation to the metatarsus. In embryo XXIIa, this axis passed to the cranial side of the first metatarsal whereas in embryo XXIII, it passed between the first and second metatarsals (Figs 23B and C). Despite the increased divergence of the first metatarsal, the angles between the first and second metatarsals and between the second and third metatarsals were virtually the same as in embryo XXIIa (see Table 3).

Fig 24. Size, shape and relationships of the embryonic skeletal elements (plantar views, drawn from the transparency reconstructions) compared to the adult foot.

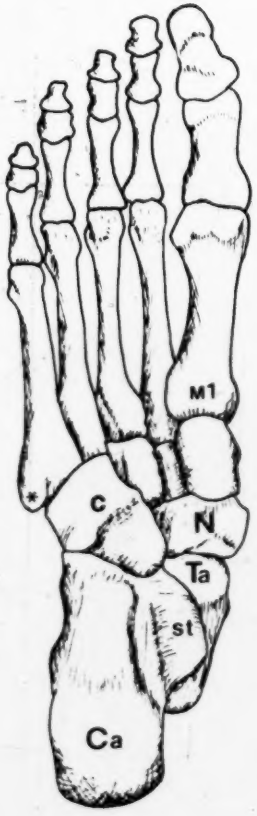
A) Adult, right foot.
B) Embryo XXIIa, right foot.
C) Embryo XXIII, left foot.

The toes of embryo XXIII have not been represented because they were damaged in the serial sections and could not be included in the transparency reconstruction. In embryo XXIIa, only the proximal and second phalanges are chondrified.

As in figure 23, the embryonic calcaneus (Ca) appears to be situated on the fibular side of the talus (Ta), although in a more plantar plane.

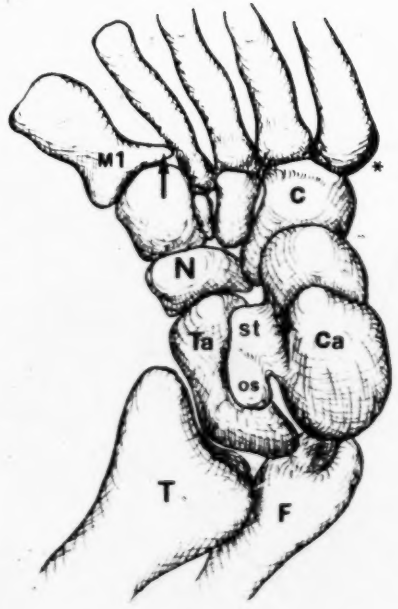
In embryo XXIII, the accessory ossicle (os) fused to the posterior edge of the sustentaculum tali (st) is shown.

Observe that the first metatarsal (M1) in the embryonic foot demonstrates a long process on the fibular side of its base where the peroneus longus tendon attaches (arrow). In the adult foot, this process is absent. The tuberosity of the base of the fifth metatarsal (*) which is seen in the adult foot, is not apparent in the embryonic skeletons.



A

B



C

However the shafts of the outer four metatarsals no longer appeared straight as in embryo XXIIa, but were bowed towards the first metatarsal head (Fig 23). This bowing was most pronounced in the second metatarsal and decreased progressively in the more fibular metatarsals. As a result, the entire forefoot was markedly adducted toward the tibia, giving the foot a convex fibular border and a concave tibial border (see Fig 18C). It should be noted that this postural feature was less apparent in the individual serial sections than in the transparency reconstructions.

In the midfoot, there were no appreciable differences between the embryonic and adult specimens in the shape, size and arrangement of the cuboid, navicular and cuneiforms bones (Figs 23 and 24).

In the hindfoot, fibular and dorsal views revealed that the shape of the embryonic calcaneus was very similar to the adult (Figs 21D and 23). Even at stage 20, the anterior process, sustentaculum tali and calcaneal tuberosity, although not yet chondrified, had a well defined precartilaginous form and the calcaneal sulcus was readily apparent (Fig 19A).

At all four embryonic stages, the calcaneus was proportionately shorter than the adult condition where it was 45% longer than the talus (see Table 3). In both embryos XXa and XXI, the calcaneus was the same length as the adjacent talus and in XXIIa, it was actually 14% shorter than the talus. However, in embryo XXIII, the calcaneus was

5% longer than the talus, which was the first indication that it had begun to grow relatively faster than the talus and towards its adult proportions.

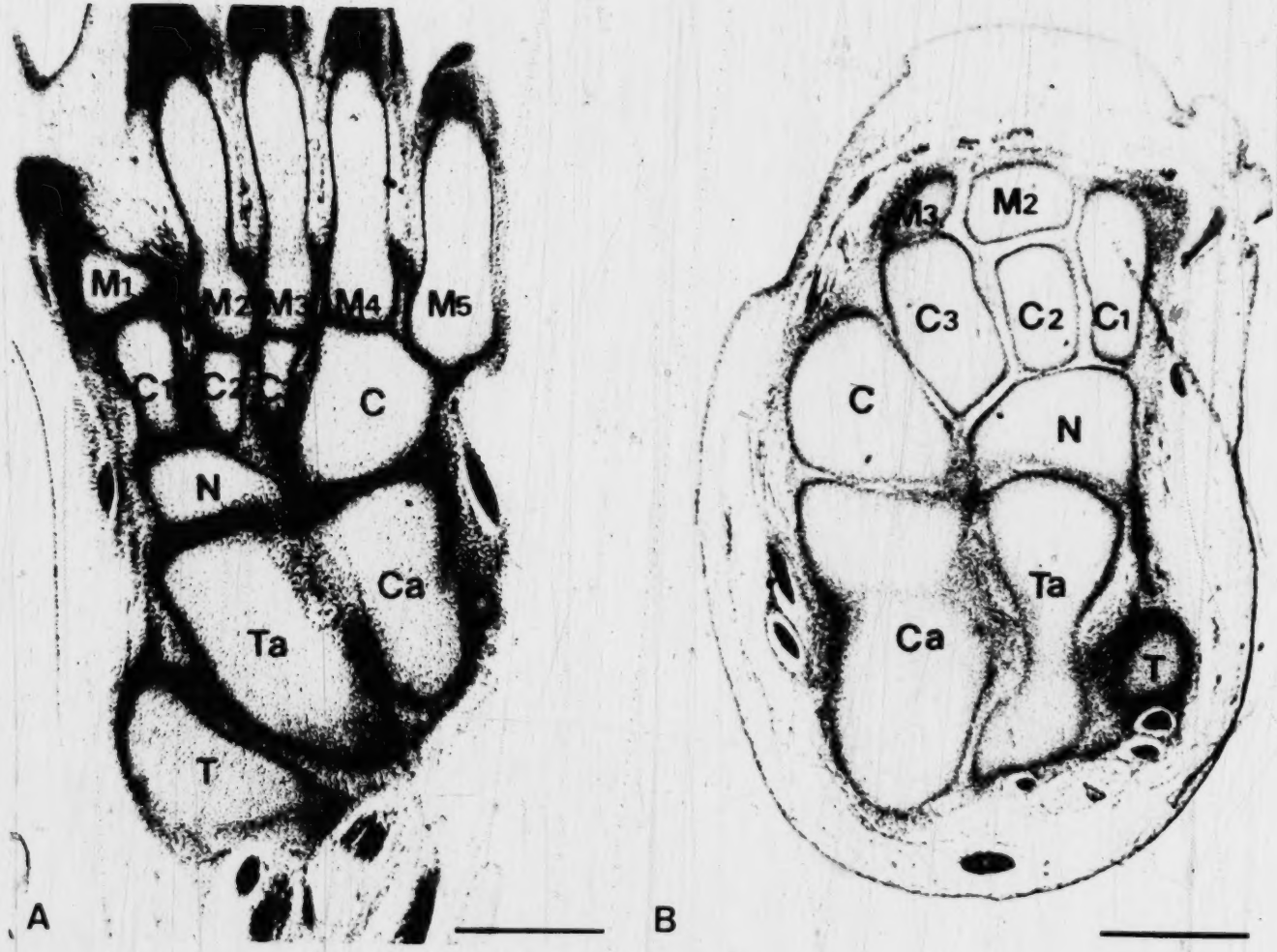
Not only were the relative sizes of the calcaneus and talus different from the adult situation, their orientation to each other appeared to be quite different. From a dorsal view, the adult talus is superimposed on the calcaneus, obscuring the calcaneal sulcus. However, figures 23 and 24 present the embryonic calcaneus on the fibular side of the talus, although in a somewhat more plantar plane, and demonstrate an exposed calcaneal sulcus.

This unusual talocalcaneal relationship was depicted also in the horizontal sections of embryos XXIIa and XXIII (Fig 25) as well as the posterior view of the wax model (Fig 26A). In addition, this view suggested that the tibia extended further plantarward than the fibula, which is the exact opposite of the adult situation where the fibula is longer (Fig 26D). Therefore, the initial impression of the horizontally-sectioned embryos, from both the serial sections and the reconstructions, was that the calcaneus was situated beside the talus and that the tibia extended further than the fibula.

However, these observations were made with the sole of the foot directed downward, as if the foot was in the anatomical position. When the relationships of the skeletal elements were reconsidered bearing in mind that the first metatarsal was actually directed cranially, the arrangement

Fig 25. Photomicrographs demonstrating size, shape and relationships of the embryonic skeletal elements.
A) Embryo XXIIa, right foot.
B) Embryo XXIII, left foot.

These horizontal sections (viewed from above) seem to show that the calcaneus (Ca) is situated on the fibular side of the talus (Ta). These sections pass through the tibial malleolus (T) but below the fibular malleolus suggesting that the tibial malleolus extends the further of the two.


M1
M2
M3
M4
M5
C1
C2
C3
C
N
Ca
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M3
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C1
C
N
Ta
Ca
T
B

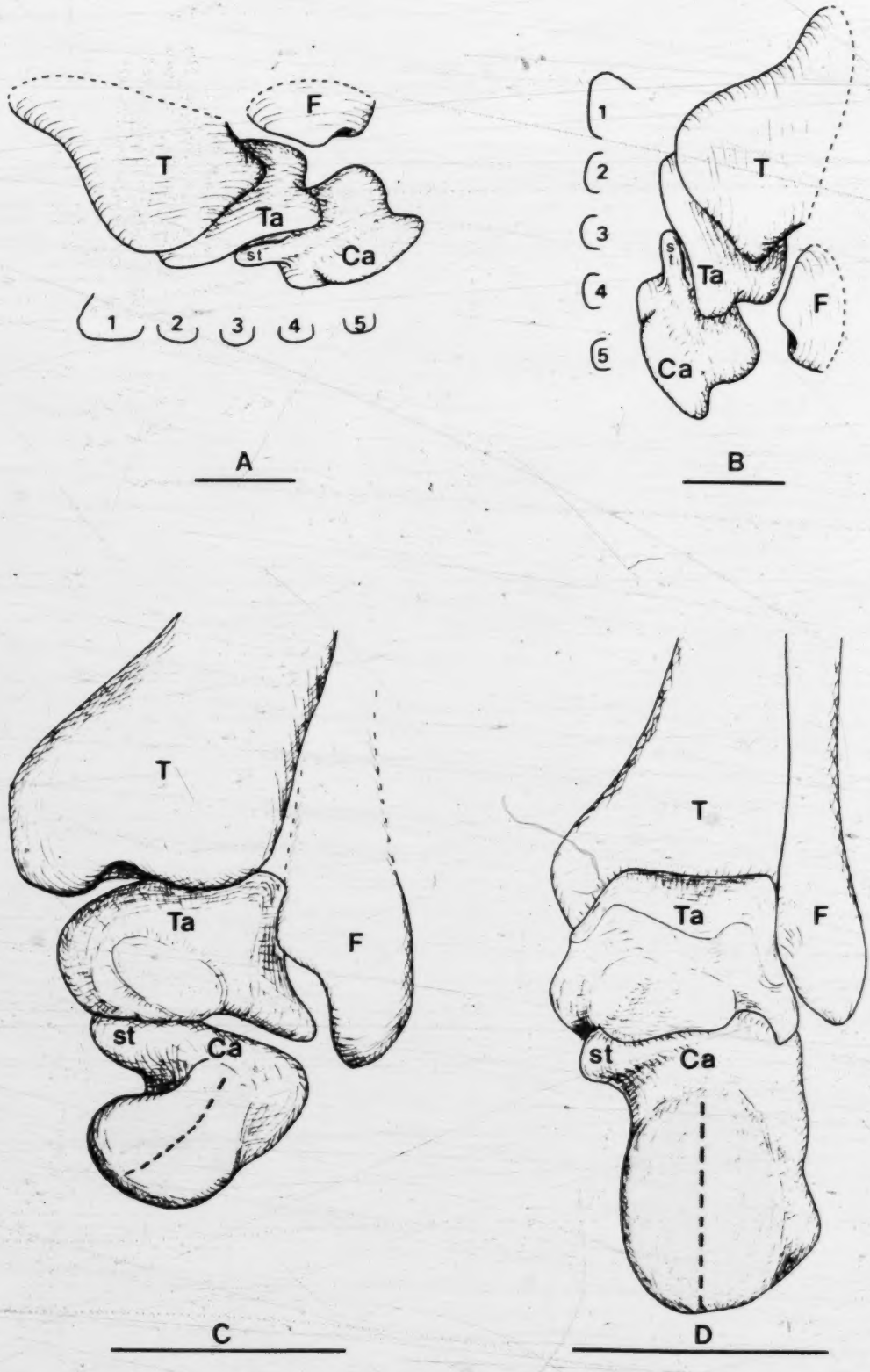
Fig 26. Skeletal elements of the right hindfoot, comparing embryonic and adult feet (posterior views).

A) Embryo XXIIa.
Drawn from the wax model oriented with the sole of the foot directed downward and the metatarsal heads (1 - 5) in the horizontal plane, as in the anatomical position. This view suggests that the calcaneus (Ca) is situated on the fibular side of the talus (Ta) and that the tibia (T) extends further than the fibula (F).

B) Embryo XXIIa.
Drawn from the wax model oriented with the sole of the foot facing medially and the first metatarsal (M1) directed cranially as in the embryonic position. This view suggests that the calcaneus is situated below the talus and that the fibula extends further than the tibia. These features are similar to the adult condition. However, unlike the adult foot, the metatarsal heads and the sustentaculum tali (st) are situated in the sagittal plane (see also Fig 26C).

C) Embryo XXI.
Drawn from the transparency reconstruction and demonstrating that when the skeletal elements of the hindfoot are examined in relationship to the ankle joint, the arrangement is similar to the adult situation. The differences between embryo XXI and the adult foot (D) include: the longer fibular malleolus; the upwards tilt of the sustentaculum tali; and the inversion and smaller proportions of the calcaneal tuberosity (shaded area).

D) The Adult Right Foot.
Note the horizontal plane of the sustentaculum tali and the vertical orientation of the long axis of the calcaneal tuberosity (broken line).


F
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Ta
st
Ca
1
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Ta
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st
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C
T
Ta
F
st
Ca
D

seemed to be completely different (Fig 26B). Now, the posterior view of the wax model showed the talus superimposed on the calcaneus and the fibula extending further than the tibia. From this orientation, the relationships of the skeletal elements of the hindfoot appeared to be quite similar to the adult situation but the forefoot seemed to be markedly inverted relative to the hindfoot and the sustentaculum tali was tilted upwards. Therefore, two different and conflicting interpretations could be made from the wax model: one based on the forefoot oriented in the horizontal plane as in the anatomical position (Fig 26A); the other based on the great toe directed cranially (Fig 26B).

This conflict was resolved by studying the transparency reconstruction of the coronally-sectioned embryo XXI. In this model, the orientation of the talus to the calcaneus was represented in relation to the ankle joint. It confirmed that the general arrangement of the hindfoot elements was similar to the adult situation, although, subtle differences also existed (Figs 26C and D). As in the adult foot, the body of the embryonic talus was situated in the mortice formed by the tibia and fibula. The same arrangement was also observed in the coronal sections of embryos XXa and XXIIa (Fig 27).

The model of embryo XXI also demonstrated that the fibular malleolus, articulating with the concave facet of the lateral process of the talus, extended past the tip of

Fig 27. Photomicrographs of coronal sections through the hindfoot, demonstrating relationships of the embryonic skeletal elements.

A) Embryo XXa, right foot, viewed from behind.
B) Embryo XXI, right foot, viewed from behind.
C) Embryo XXIIa, left foot, viewed from the front.

All three sections clearly demonstrate that the calcaneus (Ca) is situated below the talus (Ta) and that the fibula (F) extends further than the tibia (T), as in the adult foot.

A

B

C

the tibial malleolus (Fig 26C). There was no evidence of the fibula articulating with the calcaneus.

The proximity of the fibular malleolus to the calcaneus was also examined from the sagittal sections of XXa and XXIIb. Both of these specimens demonstrated the close proximity of the tip of the malleolus to the upper surface of the calcaneus. However, direct contact between the two bones was not detected (Figs 19A and B).

Although the model of embryo XXI confirmed that the talus was situated above the calcaneus, there was evidence to indicate that the talocalcaneal relationship was not identical to the adult foot. Compared to the adult situation, the sustentaculum tali was tilted upwards and the calcaneal tuberosity was markedly inverted (Fig 26C and D). In addition, the calcaneal sulcus was directed outwards rather than up towards the talus and the cervical ligament was very prominent rather than being buried in the tarsal sinus (Fig 28). Together, these observations provided a good indication that the calcaneus was inverted below the talus (i.e. laterally rotated) compared to the anatomical position. To achieve the same orientation as the adult foot, the calcaneus would have to medially rotate around its long axis.

Another difference between embryo XXI and the adult foot was the orientation of the talar head. In the embryo, the long axis of the talar head was approximately parallel to the trochlear surface of the talus whereas in the adult

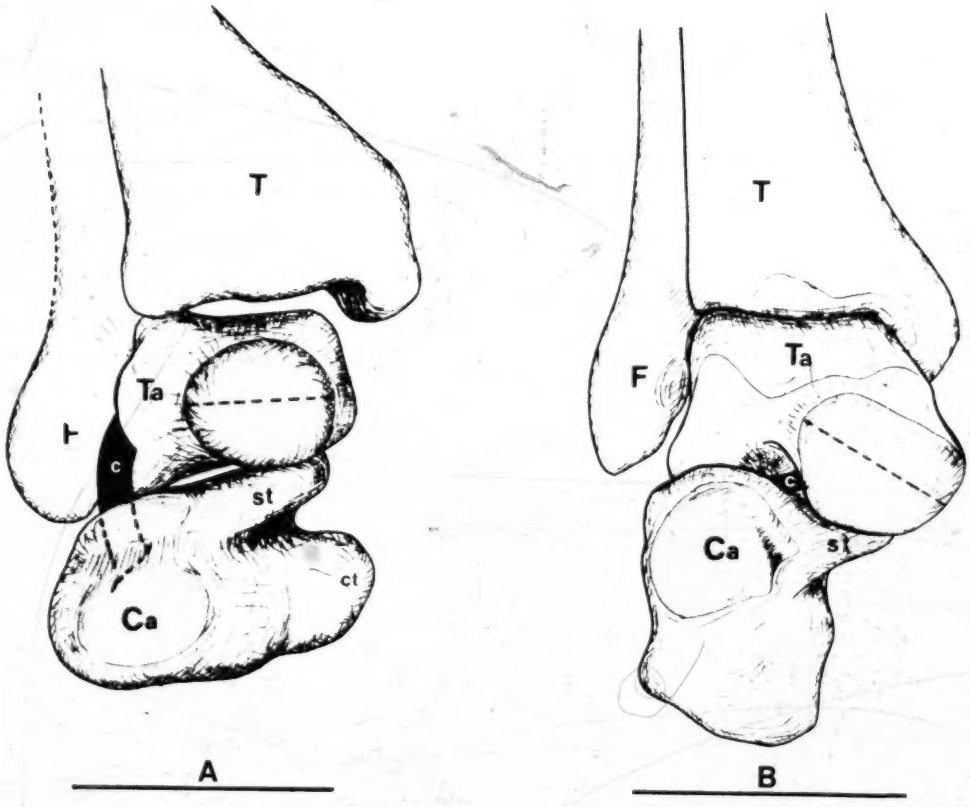


Fig 28. Comparison of embryonic and adult skeletal relationships in the hindfoot.
Anterior views of the tibia (T), fibula (F), talus (Ta) and calcaneus (Ca) at the level of the talonavicular and calcaneocuboid joints. Shaded areas represent the articular surfaces for the navicular and cuboid.

A) Embryo XXI.
Drawn from the transparency reconstruction to demonstrate: the apparently horizontal plane of the long axis of the talar head (broken line); the prominence of the cervical ligament (c); the upwards tilt of the sustentaculum tali (st); the inversion of the calcaneal tuberosity (ct).
B) The adult foot.
Observe the oblique orientation of the long axis of the talar head (broken line); the cervical ligament almost completely buried in the tarsal sinus; the horizontal orientation of the sustentaculum tali; the medial tilt of the upper aspect of the calcaneal facet for the cuboid.

foot, the long axis had an oblique orientation (Fig 28).

To examine the embryonic orientation of the forefoot to the hindfoot, one of the tracings through the metatarsal shafts was superimposed in its aligned position onto the tracings of the bones of the hindfoot (Fig 29). Whereas in the adult foot the line intersecting the first and fifth metatarsals was perpendicular to the long axis of the leg (Fig 29D), in embryo XXI, the line was inverted 35° from the theoretical weight-bearing plane of the foot (see Figs 9K and 29A). Furthermore, this line was approximately parallel to the sustentacalum tali indicating that the metatarsals and calcaneus were both inverted to about the same extent.

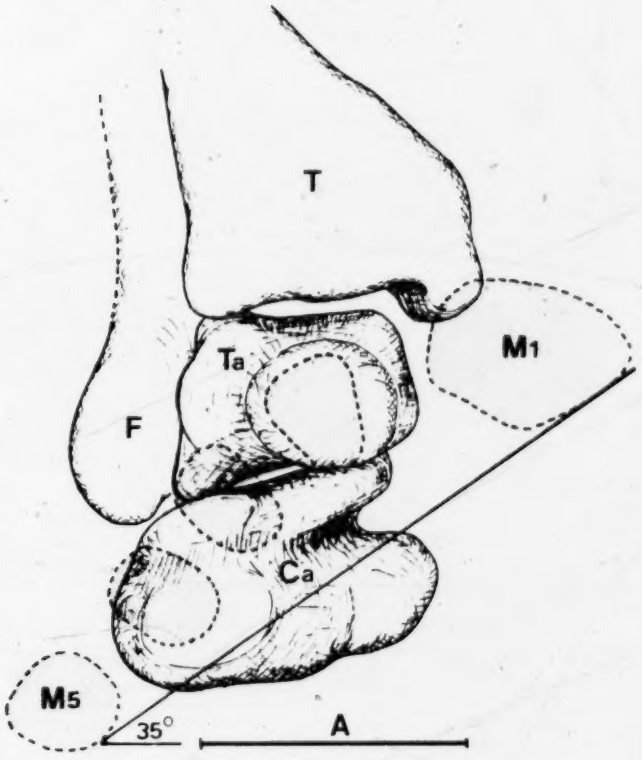
In addition to the observations pertaining to the skeletal elements, the transparency models also demonstrated that all the major ligaments in the foot could be discerned as early as stage 20 and from all appearances had the same points of attachment as in the adult foot (Figs 30 and 31).

Fig 29. Hindfoot-forefoot relationship.

A) Embryo **XXI**, right foot viewed from the front, drawn from the transparency reconstruction.
By superimposing a tracing through the metatarsal shafts (shaded) in its aligned position onto the bones of the hindfoot, forefoot inversion relative to the trochlear surface of the talus (Ta) is demonstrated. Note also the inverted position of the calcaneus (Ca) below the talus.

B)Embryo **XXIIa**, right foot, antero-dorsal view, drawn from the wax model. This view demonstrates the trochlear surface (arrow) of the talus and the inversion of the forefoot in relation to the ankle joint.

C) Adult, right foot, viewed from behind.
In the weight-bearing anatomical position, the metatarsal heads are perpendicular to the long axis of the leg.


T
Ta
M1
F
Ca
M5
35°
A

T
F
Ta
Ca
N
C
C
C
C
M1
B

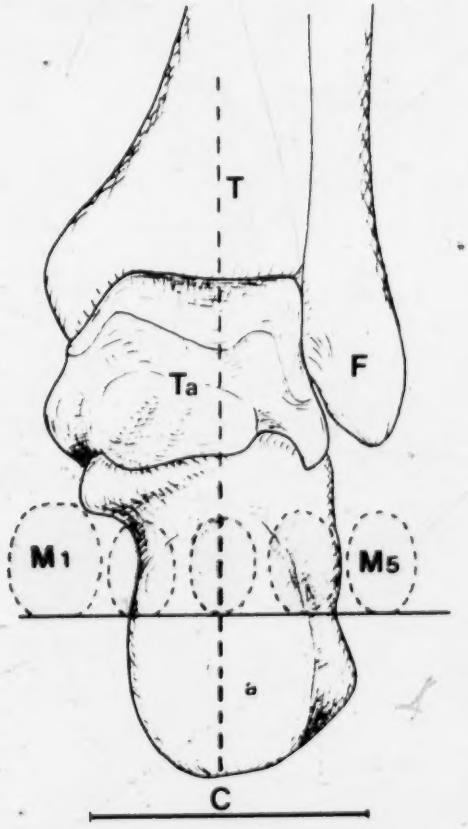

T
Ta
F
M1
M5
C

Fig 30. Skeletal elements of the hindfoot of embryo XXI.

Views of the tibia (T), fibula (F), talus (Ta) and calcaneus (Ca) and some of the related ligaments, drawn from the transparency reconstruction. Shaded areas represent the cut faces of the tibia and fibula which are incompletely represented.

A) Antero-fibular view.
Observe: the shape of the trochlear surface of the talus; the apparent absence of concavity on the fibular side of the talus whereas the adult foot shows a constricted talar neck (see Fig 28B); the outwards (fibular) orientation of the calcaneal sulcus (arrow) to which the prominent cervical ligament (c) is attached.

B) Posterofibular view.
Observe the shape of the ankle and subtalar joints.

C) Fibular view.
Observe the inversion of the calcaneal tuberosity; the outwards orientation of the calcaneal sulcus (arrow) to which the cervical ligament is attached; the broad calcaneofibular ligament (CaF); and the posterior talofibular ligment (pTaF).

D) Similar to C) but without the fibula to show the fibular side of the talus.

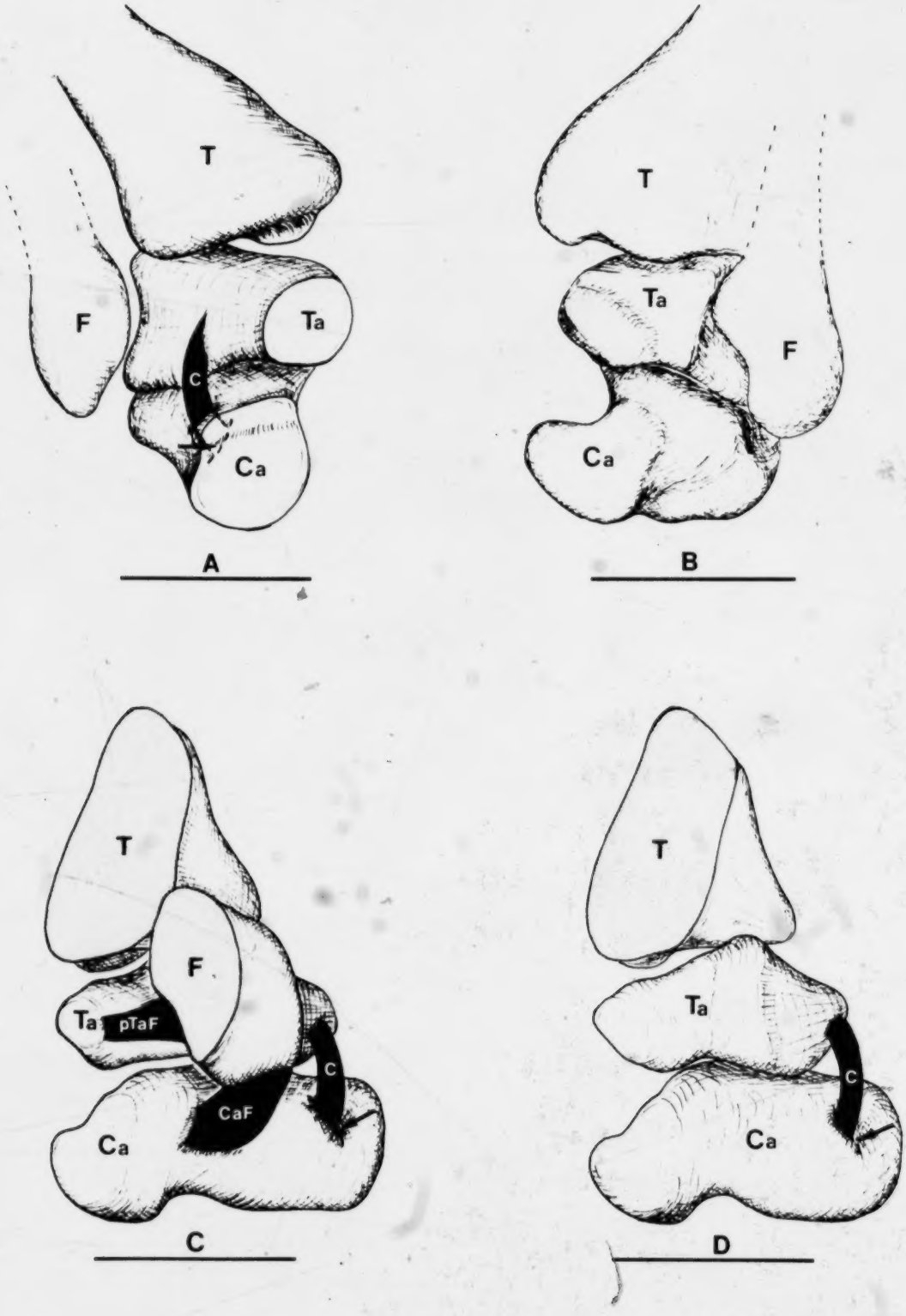
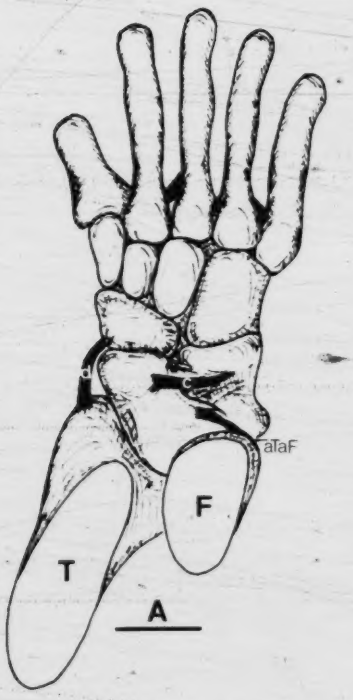

T
F
Ta
C
Ca
A
T
Ta
F
Ca
B
T
F
Ta
pTaF
C
CaF
Ca
C
T
Ta
C
Ca
D

Fig 31. Ligaments of the foot and ankle region of the embryonic foot:

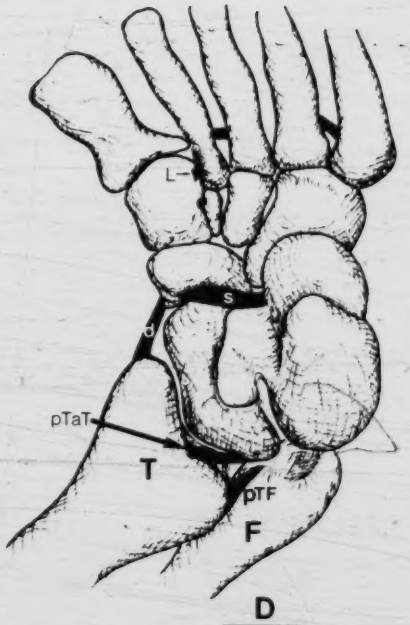
deltoid (d), anterior talofibular (aTaF), anterior tibiofibular (aTF), posterior talofibular (pTaF), posterior talotibial (pTaT), posterior tibiofibular (pTF), cervical (c), bifurcate (b), Lisfranc (L), plantar calcaneonavicular or spring (s). Also shown are interosseous membrane (im) and the ligaments between the metatarsals.



A

B

C



D

In summary, the following features were observed in the skeleton of the embryonic foot:

1. the phalanges as the last elements to chondrify, did so in a proximodistal sequence
2. a well-developed fibular longitudinal arch as in the adult foot but no arch along the tibial side of the foot
3. a transverse arch through the midfoot, similar to the adult condition
4. the forefoot of stage 22 characterized by fan-spread metatarsals and digits in addition to a short, divergent first toe
5. the first metatarsal of stage 23 extended almost as far distally as the second metatarsal and the outer four metatarsals bowed towards the first metatarsal
6. inversion of the forefoot
7. a proportionately short calcaneus in relation to the talus when compared to the adult foot
8. the calcaneus situated below the talus as in the adult foot but laterally rotated (inverted) as indicated by: the upwards tilt of the sustentaculum tali; inversion of the calcaneal tuberosity; fibular orientation and increased exposure of the calcaneal sulcus; prominence of the cervical ligament;
9. the horizontal orientation of the long axis of the talar head
10. the fibula extending further plantarward than the tibia as in the adult foot

C. THE EXTRINSIC MUSCLES

The descriptions of the extrinsic muscles will focus on the course and attachments of the tendons in the foot. As early as stage 20, all the tendons of the extrinsic muscles, with the exception of peroneus tertius, could be identified in the ankle region with an arrangement identical to the adult condition (Fig 32). However, in almost every instance there were at least subtle differences, particularly at the distal attachment site. It should be noted that the tendon of plantaris, which was observed as early as stage 20, will not be described because it is generally regarded as insignificant and variable and is often absent. All of the remaining extrinsic tendons will be described in turn.

As in the adult limb, the calcaneal tendon was the largest tendon in the embryonic foot, with its distal attachment to the posterior surface of the calcaneus (Fig 33). This attachment site, shown in figure 32A, appears to extend higher on the tibial side. In the adult limb, the fibers of the calcaneal tendon twisted approximatey 90° as they descended. Figures 34A and B show that the fibers emerging from the tibial side of the muscle became the most posterior at their attachment on the calcaneus. This phenomenon was not apparent in the embryonic limbs because the course of the tendon fibers could not be observed in the serial sections.

The embryonic tendons of the deep plantar flexors coursed in the leg and foot similarly to the adult condition

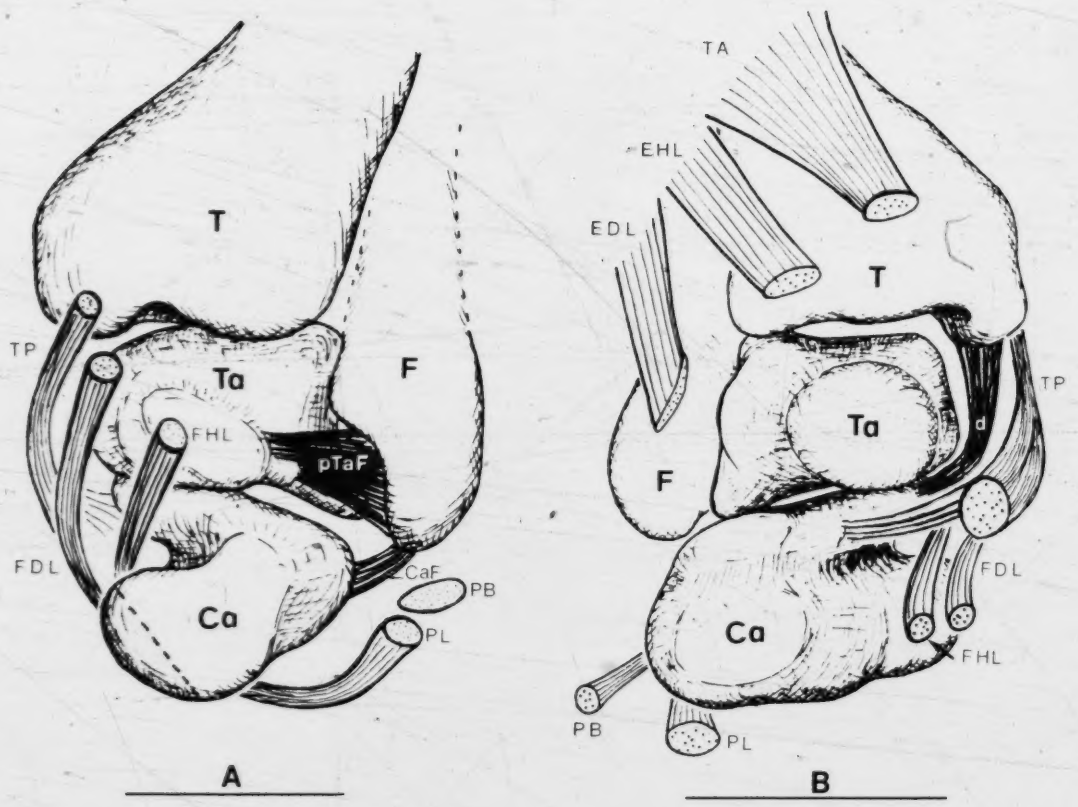


Fig 32. Tendon relationships in the right hindfoot of embryo XXI.
A) Posterior view
B) Anterior view

Shaded area represents the distal attachment site of the calcaneal tendon.
Stippled areas represent the cut ends of the tendons: peroneus brevis (PB), peroneus longus (PL), flexor hallucis longus (FHL), flexor digitorum longus (FDL), tibialis posterior (TP), tibialis anterior (TA), extensor hallucis longus (EHL), extensor digitorum longus (EDL).
Note the fibers from the tibialis posterior tendon attaching in part to the anterior aspect of the sustentaculum tali.
Also shown are the posterior talofibular (pTaF), calcaneofibular (CaF) and deltoid (d) ligaments.

Fig 33. Plantar views of embryonic extrinsic tendons and related intrinsic muscles.

A and **C**) Embryo XXIIa, right foot.
B and **D**) Embryo XXIII, left foot.

The calcaneal tendon (ct) seems to approach the calcaneus from its tibial side.

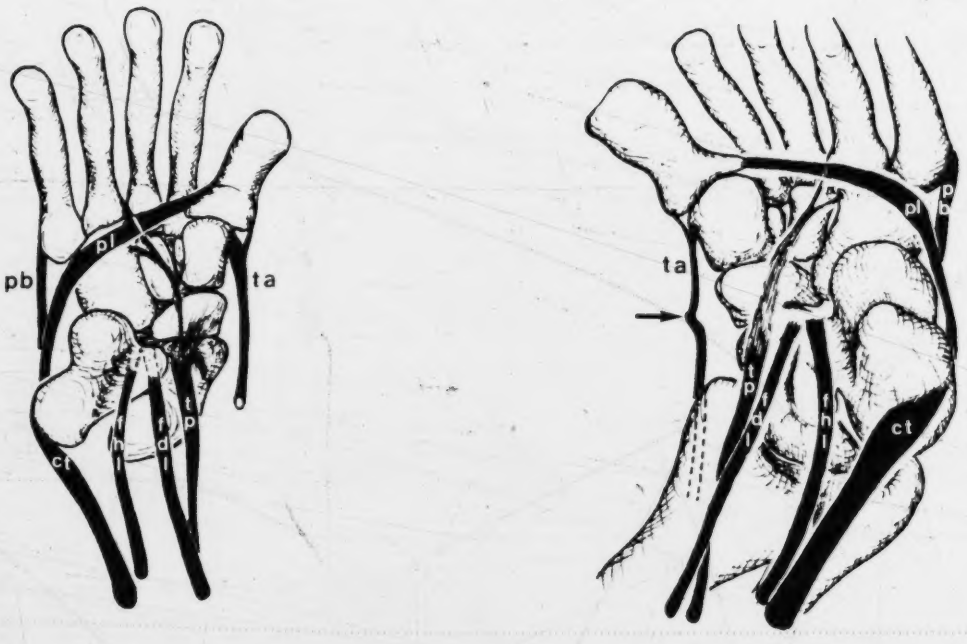
The flexor digitorum longus (fdl) and flexor hallucis longus (fhl) tendons are shown only in part in **A**, **B** and **D**. As in the adult foot, fhl courses below the sustentaculum tali, then crosses below fdl and proceeds into the first toe.

The tibialis posterior tendon (tp) abruptly becomes more diffuse below the talar head. In both embryos, fibrous slips attach to the tibial side of the cuboid and the third cuneiform. Another distinct slip attaches to the tibial side of the base of the fourth metatarsal.

The tibialis anterior tendon (ta) attaches distally to both the first cuneiform and the base of the first metatarsal. In **B** this tendon demonstrates an undulatation (arrow) at the tibial side of the navicular.

Quadratus plantae (qp) attaches proximally to the calcaneus and distally to fhl and fdl where they cross. In embryo XXIIa, only one head of qp was seen whereas both heads were detected in embryo XXIII.

Also shown are the four lumbricals (l) arising from the tendons of fdl, then coursing into the outer four toes.


pb
pl
ta
ct
A
ta
pl
ct
B

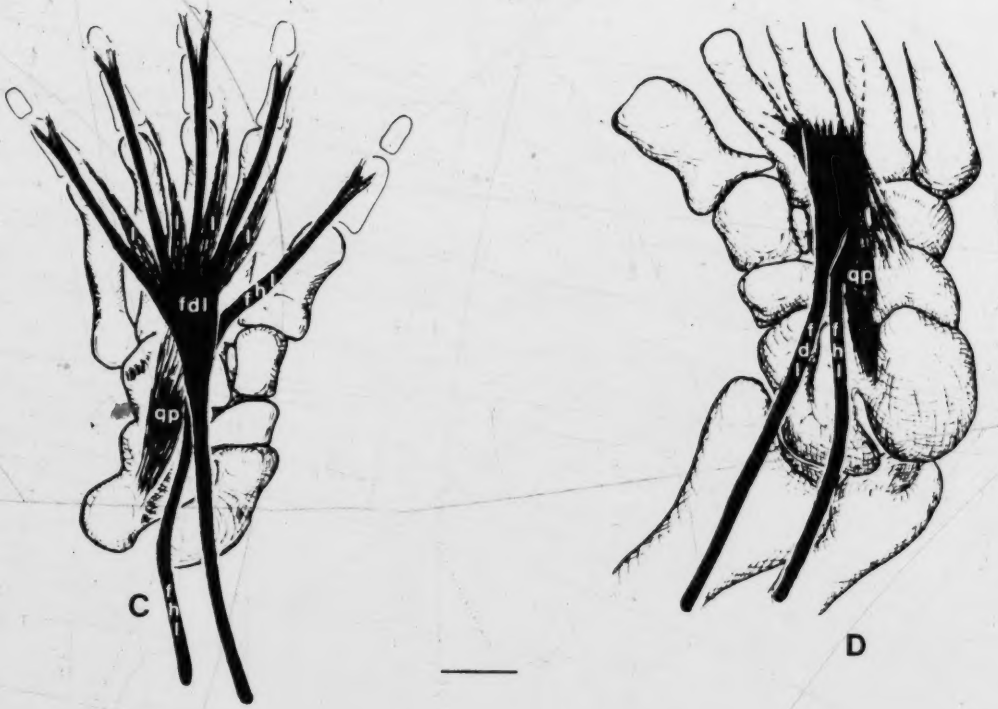
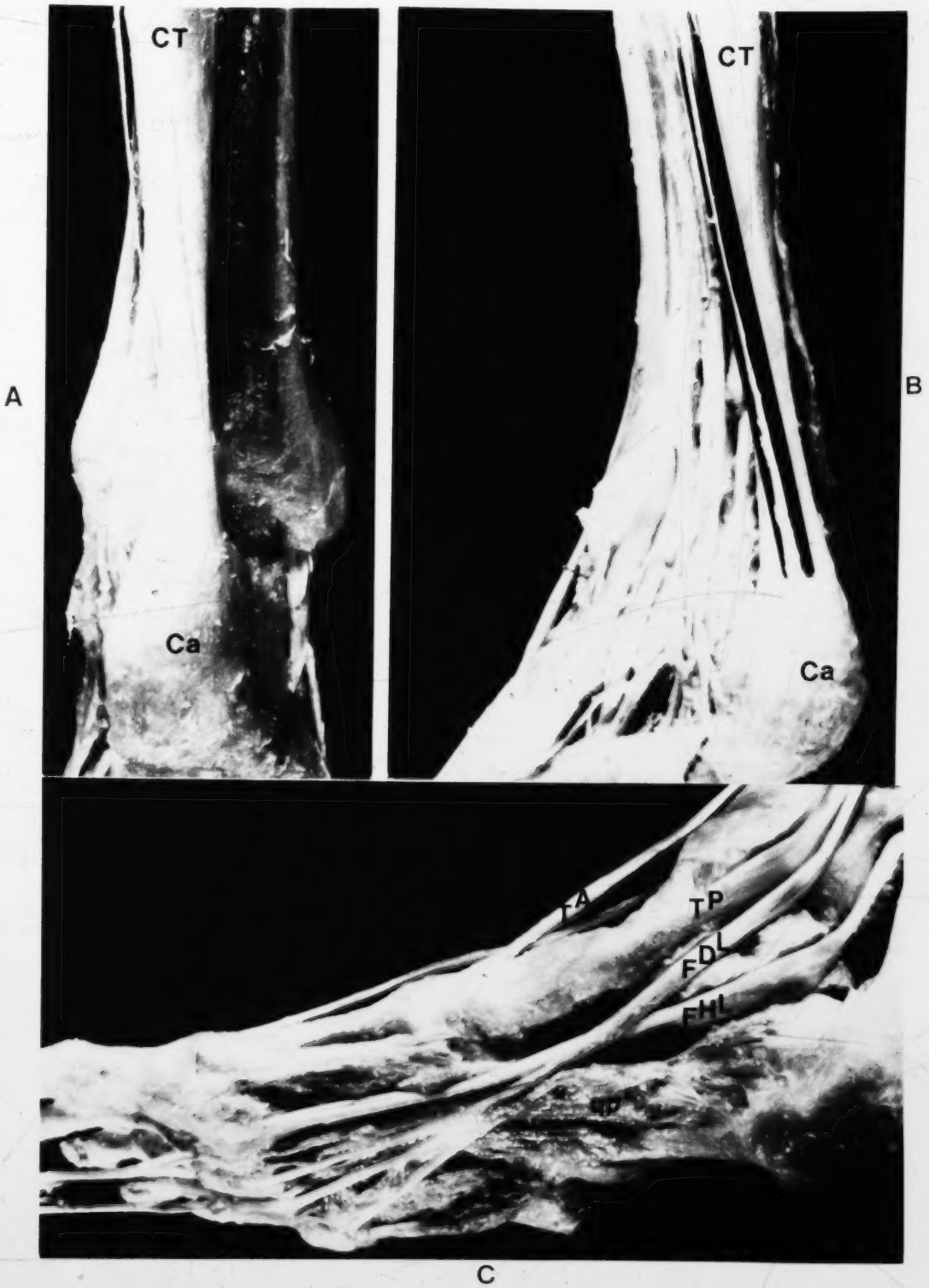

fdl
fhl
qp
C
qp
D

Fig 34. Extrinsic flexor tendons of the adult right foot.

A) Posterior view of calcaneal tendon, (CT) demonstrating torsion of its fibers.

B) Postero-medial view of calcaneal tendon demonstrating that the fibers emerging from the medial side of the muscle (raised by the black paper), attach distally to the posterior aspect of the calcaneus.

C) Medio-inferior view showing: the attachment of tibialis posterior (TP); flexor hallucis longus (FHL) coursing below the sustentaculum tali (st) then crossing under flexor digitorum longus (FDL); quadratus plantae (qp).


A
CT
Ca
B
CT
Ca
TA
TP
FDL
FHL
tp
C

(Figs 32, 33 and 34C). The related intrinsic muscles were clearly visualized in embryo XXIIa. As in the adult limb the quadratus plantae attached distally to the tendons of flexor digitorum longus and flexor hallucis longus and the lumbricals arose from the tendons of flexor digitorum longus (Figs 33C, 34C and 35). Even the passage of the tendons of flexor digitorum longus through the bifurcated tendons of flexor digitorum brevis was apparent in embryo XXIIa (Fig 35A). However, the termination of the long flexor tendons in the toes was not well-defined in any of the embryos. In both embryos XXIIb and XXIII, the toes were damaged so that the distal attachment of these tendons could not be observed. In the younger specimens, the tendons merged with the mesenchymal condensation representing the unchondrified middle and distal phalanges (see Fig 19A). The precartilaginous nature of the phalanges to which these tendons would eventually attach suggested that the tendons might not yet be firmly anchored distally, in stages 20 through 22. Figure 35C demonstrates the undulating course of the flexor digitorum longus tendon seen in embryo XXa.

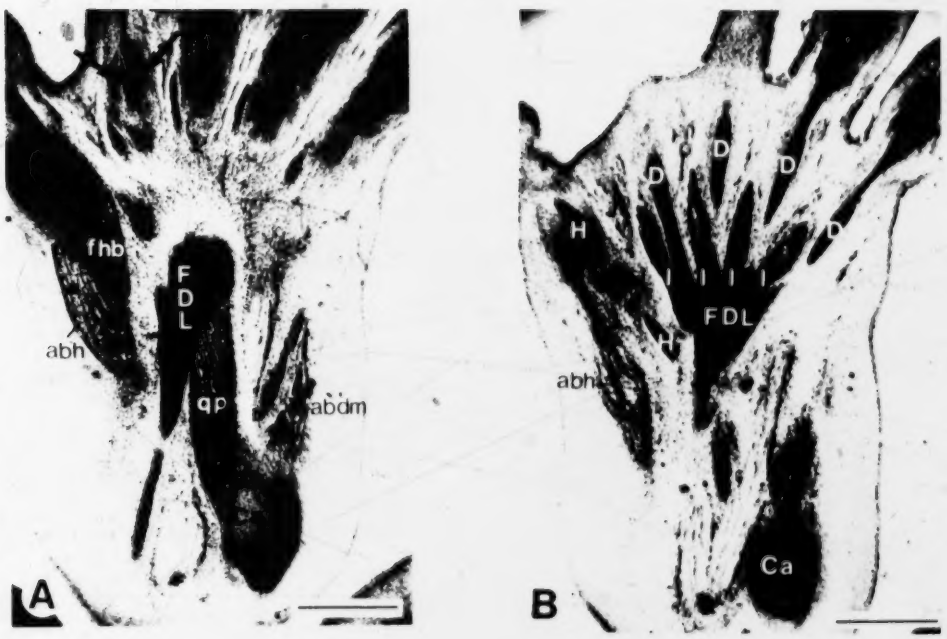
The distal attachment of embryonic tibialis posterior was the source of some initial confusion because primary termination of the fibers on the navicular, as seen in the adult foot, was not readily apparent. Rather, the tendon flared out proximal to the navicular and then appeared to end on a mesenchymal condensation deep to the head of talus. This condensation was particularily well defined in the

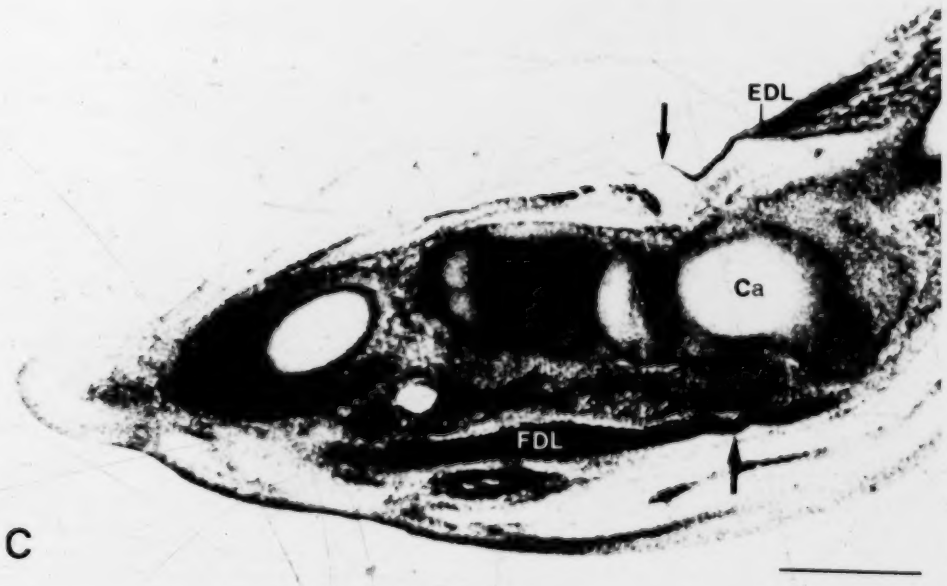
Fig 35 Photomicrographs of demonstrating the morphology of the extrinsic tendons of the toes and related intrinsic muscles.

A) Embryo **XXIIa**, right foot, horizontal section viewed from above.
Flexor digitorum longus (FDL) to which quadratus plantae (qp) attached. More distally, the digital tendons of FDL (arrowhead) pass through the bifurcation (arrows) in the tendons of flexor digitorum brevis. Note that both quadratus plantae and abductor digiti minimi (abdm) attach proximally to the calcaneus (Ca). Also shown is a portion of abductor hallucis (abh). Distally it fuses with the tibial head of flexor hallucis brevis (fbh).

B) Embryo **XXIIa**, right foot, horizontal section viewed from above.
The digital tendons (D) of flexor digitorum longus (FDL) give rise to the four lumbricals (l). Also shown is the tendon of flexor hallucis longus (H).

C) Embryo **XXa**, right foot, sagittal section viewed from the tibial side.
The broad tendon of flexor digitorum longus (FDL) is compared to the attenuated tendon of extensor digitorum longus (EHL). Both tendons demonstrate undulations (arrows).


fhb
F
D
L
abh
qp
abdm
A
D
D
D
D
H
FDL
abh
Ca
B


EDL
Ca
FDL
C

horizontal-sections of embryos XXIIa and XXIII (Figs 36A and B). Upon closer examination at higher magnification, it was realized that the fibers had not ended but had abruptly become more diffuse. These less condensed fibers radiated from the mesenchymal condensation deep to the talar head (Fig 36A) and attached to the tuberosity of the navicular, the first cuneiform and the sustentaculum tali (Figs 36D and 37). Some of the fibers also blended with the spring and deltoid ligaments (Fig 37B). In addition to the diffuse, generalized attachment of this tendon, the horizontally-sectioned specimens (embryos XXIIa and XXIII) demonstrated slender, condensed fibrous slips attaching to the cuboid, third cuneiform and the base of the fourth metatarsal (Figs 36C and 38). Ultimately, it was concluded that the termination of embryonic tibialis posterior (Fig 38) was virtually the same as the adult. However, quite unlike the adult foot, the most proximal extent of abductor hallucis attached to the tendon of tibialis posterior in the vicinity of the talonavicular joint (Fig 37D). In the adult foot, no adherence between abductor hallucis and the tendon of tibialis posterior was seen (Fig 49A).

The embryonic tendon of tibialis anterior coursed obliquely from the dorsum to the plantar aspect of the tibial side of the foot and terminated in the region of the first cuneometatarsal articulation as in the adult foot (Figs 33, 39 and 40). In the three older specimens (embryos XXIIa and b and XXIII), where the distal attachment was

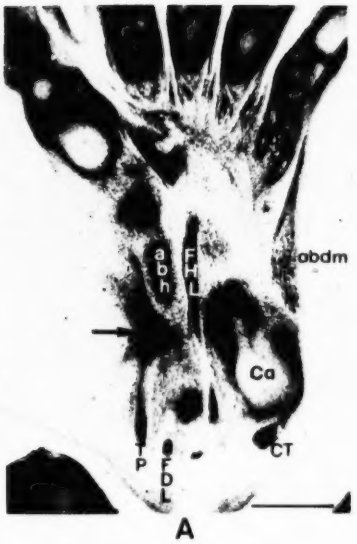
Fig 36. Photomicrographs demonstrating the morphology and attachments of the tibialis posterior tendon.

A) Embryo XXIIa, right foot, horizontal section viewed from above.
The tendon seems to terminate suddenly on a mesenchymal condensation (arrow) from which less dense fibers radiate.

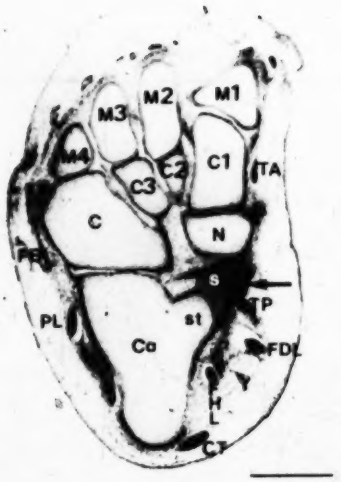
B). Embryo XXIII, left foot, horizontal section viewed from above.
As in **A**, the tendon appears to terminate on a mesenchymal condensation (arrow) in the vicinity of the spring ligament (s).

C) Embryo XXIII, left foot, horizontal plane viewed from above
A slightly deeper plane to **B**) showing a fibrous slip (arrow) of tibialis posterior attaching to the third cuneiform (C3) and the base of the fourth metatarsal (M4).

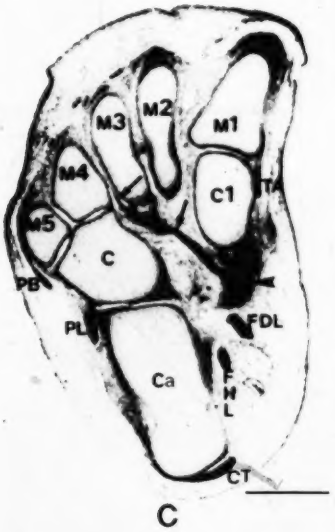
D) Embryo XXIIb, right foot, sagittal section viewed from the tibial side.
Observe the tendon of tibialis posterior flaring out and becoming abruptly more diffuse below the talar head (Ta). Less condensed fibers are attaching to the navicular (N) and the first cuneiform (C1).


abdm
a
b
h
F
H
L
Ca
CT
T
P
F
D
L

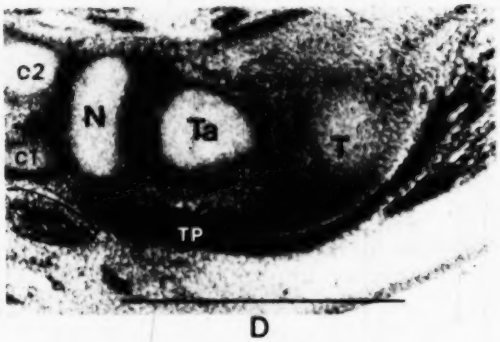
A


M3
M2
M1
M4
C2
C1
TA
C3
C
N
PB
S
TP
PL
st
Ca
FDL
H
L
CT

B


M3
M2
M1
M4
C1
TA
M5
C
PB
PL
FDL
Ca
F
H
L
CT

C


C2
N
Ta
T
C1
TP

D

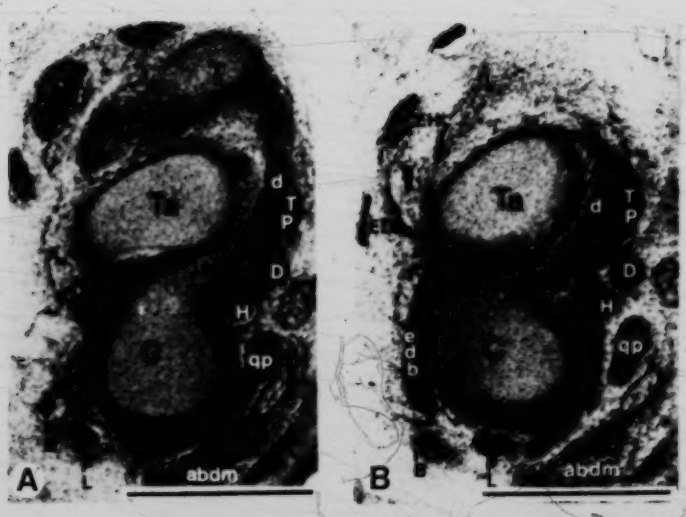
Fig 37. Photomicrographs demonstrating the morphology and attachments of the tibialis posterior tendon.

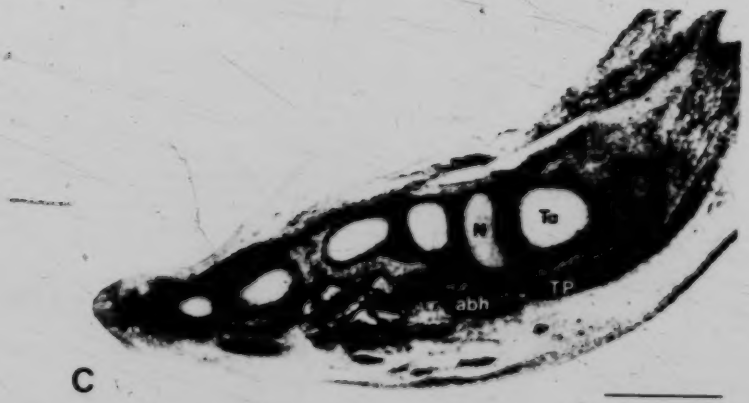
A)Embryo, right foot, coronal section viewed from the front.
This section passes through the tibia (T), talus (Ta) and calcaneus (Ca). The tendon of tibialis posterior (TP) is seen adjacent to the deltoid (d) ligament. Also shown are the tendons of flexor digitorum longus (D) and flexor hallucis longus (H).

B) Embryo XXI, right foot, coronal section viewed from the front.
A more distal plane than **A)** showing the flared out, more diffuse tendon of tibialis posterior incompletely separated from the deltoid ligament and with fibers attaching to the sustentaculum tali (st).

C)Embryo XXa, right foot, sagittal section viewed from the tibial side.
The tendon of tibialis posterior courses behind the tibial malleolus (T), then flares out and becomes more diffuse below the head of talus the (Ta). Note the close proximity of the abductor hallucis (abd) to the diffuse fibers of TP.

D) Embryo XXa, right foot, sagittal section viewed from the tibial side.
This section is slightly medial to the section in **C)**, showing the connection between the proximal portion of abductor hallucis and the tendon of tibialis posterior.


Ta
d
T
p
D
H
qp
abdm
A
Ta
d
T
p
D
H
qp
e
d
b
abdm
B


M
Ta
abh
TP
C

M
Ta
abh
TP
D

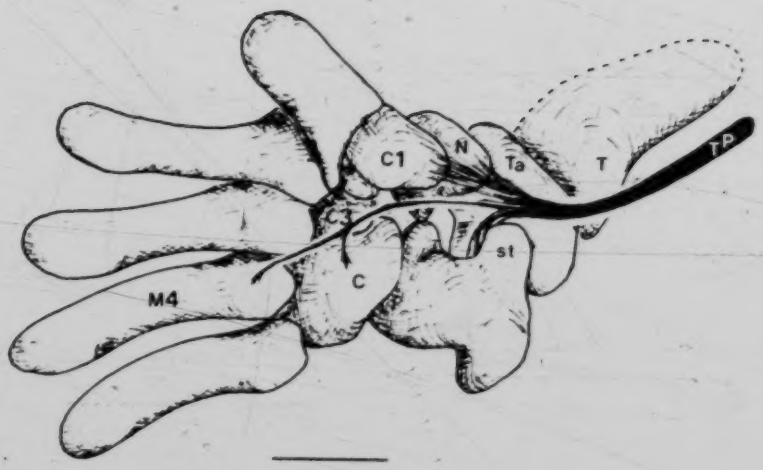


Fig 38. Course and distal attachments of the embryonic tibialis posterior.

Embryo XXIIa, antero-inferior view.
The tendon of tibialis posterior (TP) becomes abruptly more diffuse below the talar head (Ta) after which fibers attach to the sustentaculum tali (st), navicular (N), first cuneiform (C1), anterior aspect of the sustentaculum tali (st), third cuneiform (C3), cuboid (C) and the base of the fourth metatarsal (M4).

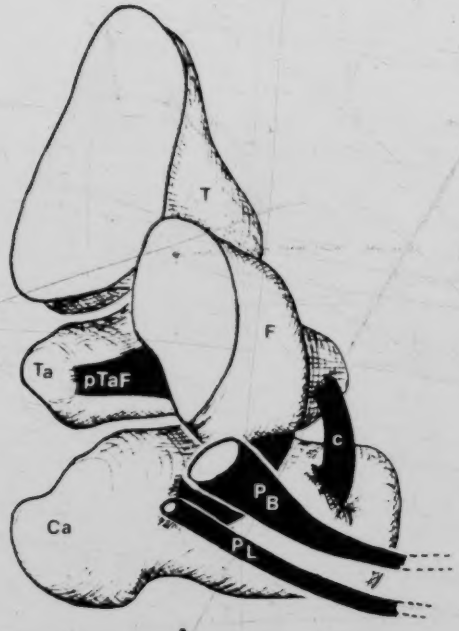
Fig 39. Course and distal attachments of the embryonic extrinsic tendons (drawn from the transparency reconstructions).

Tibialis anterior (TA), entensor hallucis longus (EHL), extendor digitorum longus (EDL), peroneus brevis (PB), peroneus longus (PL).

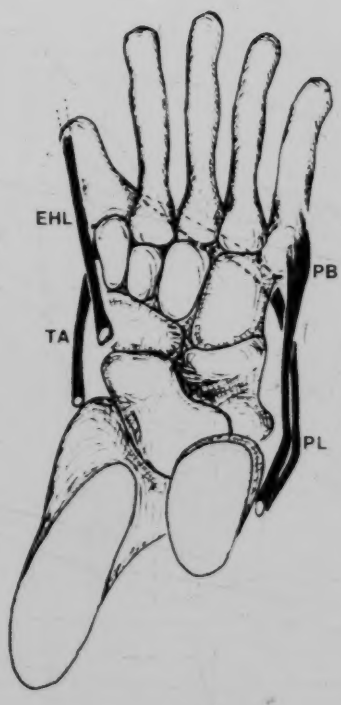
A) Embryo XXI, right foot, fibular view.
Segments of PB and PL are seen coursing over the calcaneofibular ligament, then along the fibular side of the calcaneus. Also shown are the cervical (c) and the posterior talofibular ligaments (pTaF).

B) Embryo XXIIa, right foot, dorsal view.
EDL has not been represented because it was not fully contained within the series of sections in the Shaner Collection. Most of the fibers of PB blend with the fascia overlying the fifth metatarsal. Only the most fibular fibers attach directly to the base of the fifth metatarsal.

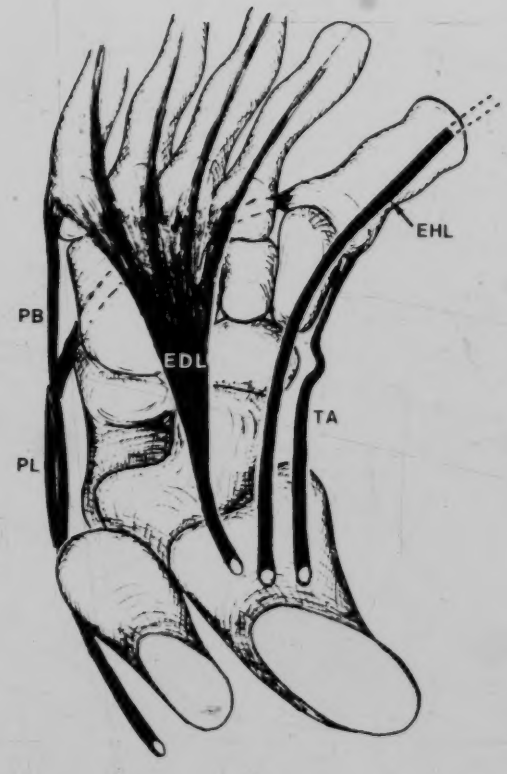
C) Embryo XXIII, left foot, dorsal view.
Note the conjoined attachment of PB and the most fibular fibers of EDL to the base of the fifth metatarsal. The tendon of TA has an undulating course beside the navicular.



A



B



C

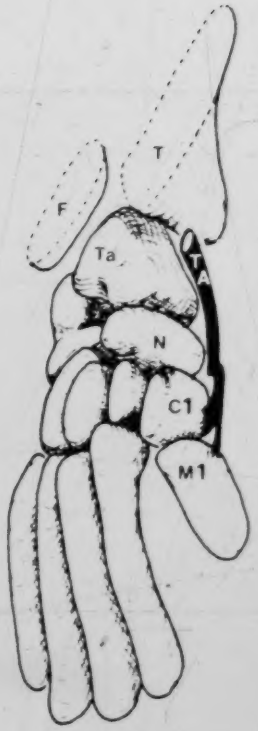
Fig 40. Course and distal attachment of the tibialis anterior tendon.

A) Embryo XXIIa, right foot, anterodorsal view.

B) Embryo XXIIa, right foot, tibial view.

C) Adult, right foot, tibial view.

In A) and B), the primary distal attachment of tibialis anterior (TA) is to the first cuneiform (C1). A fibrous slip crosses the first cuneiometatarsal interzone to attach to the tibial side of the base of the first metatarsal (M1).
In C), observe the torsion of the fibers (indicated by the red-tipped pins) and the blended attachment of TA to the first cuneiform and base of the first metatarsal.



A

B

C

better defined, the primary insertion was into the first cuneiform and a secondary fibrous slip crossed the interzone to attach to the base of the first metatarsal. However unlike the adult situation, in embryos XXa, XXIIa, XXIIb and XXIII, the tendon took a wavy course at the tibial side of the navicular (Figs 33B and 39C). In the adult foot, the fibers of the tendon were twisted, apparently due to medial torsion of the tendon around its long axis (Fig 40C).

Regarding the embryonic tendons of peroneus longus and brevis, their course and relationships in the hindfoot were basically the same as the adult situation (Figs 32, 33, and 41). However, the distal attachments of these tendons were strikingly different from the adult condition. Whereas the adult peroneus longus tendon attached distally to the first cuneiform and the base of the first metatarsal (Fig 41), in all but the stage 20 embryos, it terminated only on the first metatarsal (Figs 33A and B). As previously mentioned, this attachment site demonstrated a long, extended process which was not characteristic of the adult foot (see Fig 24).

In neither of the stage 20 embryos did the tendon of peroneus longus extend as far as the base of the first metatarsal. Unlike the older specimens, the tendon of embryos XXa and b flared out at the fibular side of the cuboid and became progressively more diffuse as it coursed across the sole toward the tibial side. In embryo XXa, the tendon appeared to fade out between the bases of the second and third metatarsals, while in embryo XXb, it seemed to

Fig 41. Course and distal attachment of the adult peroneus longus tendon.
A) Plantar view shows the tendon of peroneus longus (PL) coursing obliquely across the sole within its sheath.

B) Removal of the sheath has exposed the tendon and revealed its distal attachment to the base of the first metatarsal (M1) and the first cuneiform (C1). Also shown are the spring ligament (s) and fibrous slips of tibialis posterior (arrows).

terminate on the base of the fourth metatarsal.

In addition to the terminal attachments of the peroneus longus tendon in the six specimens described above, fibers connecting this tendon to the bases of the other metatarsals were observed in four of the embryos (Figs 42A and B). Fibers were seen attaching to the bases of metatarsal five (XXb, XXI), metatarsal four (embryos XXb, XXI, XXIIb) metatarsal three (embryos XXa, XXb, XXI, XXIIb) and metatarsal two (embryo XXIIb). Also fibers from the tendon to the third cuneiform were seen in embyro XXIIb (Fig 42D). Unfortunately, it was not readily apparent whether these slips were actually fibers of the tendon or the enclosing sheath, which in the adult foot attached to the bases of the metatarsals (Fig 41A). If the fibers extending to the metatarsals were in fact those of the sheath, then the observation would be that in these specimens, the tendon was adherent to its sheath. However, if any of these fibers continued from the tendon proper, they would represent accessory attachment slips which were not seen in the adult foot.

The difference between stage 20 (where the tendon stopped short of the first metatarsal) and stage 21 (where the tendon attached to the base of the first metatarsal) suggested that the tendon-and-sheath unit matured, coalesced or migrated from the fibular toward the tibial side of the foot, and gained attachments to the bases of the outer four metatarsals along the way. Furthermore, by the end of the

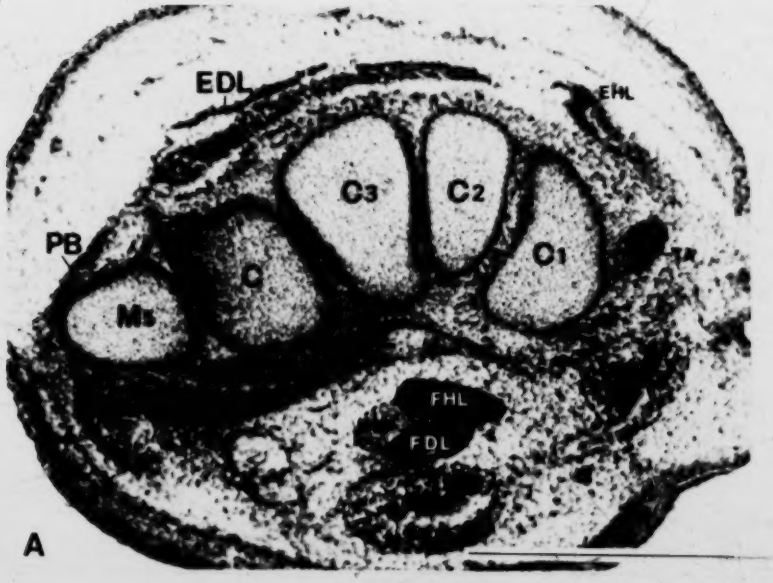
Fig 42. Photomicrographs demonstrating the embryonic peroneal tendons.

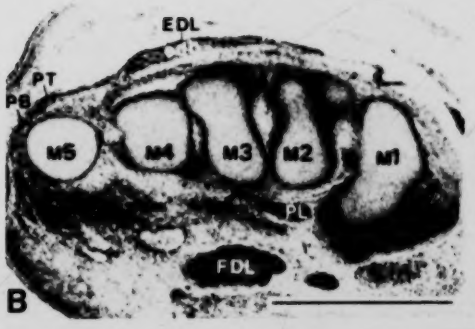
A). Embryo XXI, right midfoot, coronal section viewed from the front.
Peroneus longus is observed below the cuboid (C) with fibers (arrows) attaching to the base of the fifth metatarsal (M5). Also shown is peroneus brevis (PB), with its most fibular fibers attaching to the base of the fifth metatarsal. In the dorsum of the foot, extensor digitorum longus (EDL) is seen above the muscle belly of extensor digitorum brevis (edb).

B) Embryo XXI, right foot, coronal section distal B), passing through the metatarsals. PL is observed approaching the base of the first metatarsal with fibers (arrow) connecting it to the base of the third metatarsal (M3). In the dorsum of the foot, EDL has expanded to cover the outer four metatarsals and its most fibular fibers (representing the unseparated tendon of peroneus tertius, PT) attach to the shaft of the fifth metatarsal.

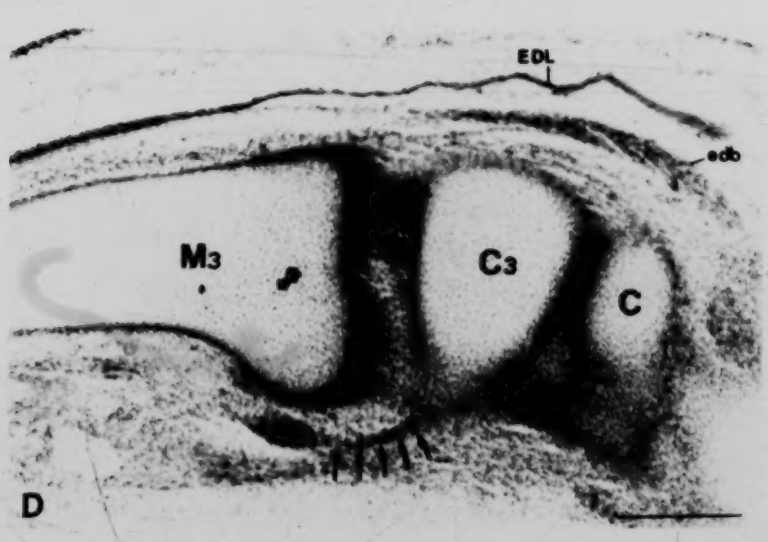
C) Embryo XXa, right foot, sagittal section, viewed from the fibular side.
The tendon of peroneus brevis (PB and arrows) courses dorsal to the fifth metatarsal (M5) and blends with the overlying mesenchymal condensation.

D). Embryo XXIIb, right foot, sagittal section viewed from the tibial side.
The tendon of PL is seen below the cuneiometatarsal joint with fibers (arrows) attaching to the third cuneiform (C3).


EDL
EHL
C3
C2
C1
PB
C
M5
TA
FHL
FDL
A


EDL
PT
PB
M5
M4
M3
M2
M1
PL
FDL
B

PB
M5
C


EDL
edb
M3
C3
C
D

embryonic period, the tendon of peroneus longus had not yet expanded its distal attachment to include the first cuneiform.

Whereas the distal attachment of the adult peroneus brevis had a broad, fanned out attachment to the tuberosity of the base of the fifth metatarsal, the embryonic tendon was not fully attached to the base of the fifth metatarsal until stage 23 (Fig 43). At stage 20, the tendon coursed dorsal to the fifth metatarsal to blend with the fascia (Fig 42C). None of the fibers actually attached directly to the metatarsal. In embryo XXb and the four older specimens, the tendon fanned out as it approached the base of the fifth metatarsal (Fig 42A) and joined with the most fibular fibers of the broad attenuated tendon of extensor digitorum longus (Figs 39C and 42B). In embryo XXI, only the most fibular fibers of the conjoined tendon attached to the base of the fifth metatarsal (Fig 42A). Over the next two stages, progressively more fibers attached to this bone (Fig 43).

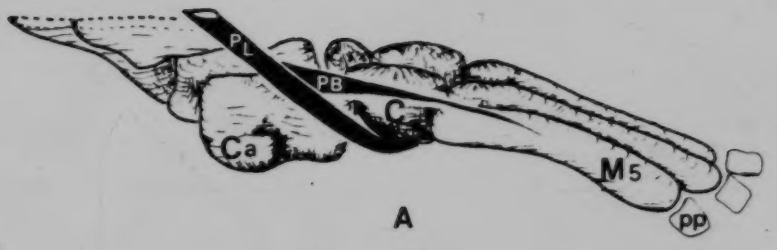
In the embryos, the long extensor tendons of the toes demonstrated an undulating course which was particularly apparent in the sagittally sectioned specimens (i.e. embryos XXa and XXIIb) (Figs 35C and 42D). This phenomenon was more pronounced in extensor digitorum longus than in extensor hallucis longus (Fig 35C). As with the long flexor tendons, the distal attachment of these tendons could not be observed due to the precartilaginous nature of the middle and distal phalanges in the younger specimens (see Fig 19A) and the

Fig 43. The embryonic peroneus brevis, acquiring increased distal attachment to the base of the fifth metatarsal over stages 20 through 23 (fibular view).

A) Stage 20. Peroneus brevis (PB) courses dorsal to the fifth metatarsal (M5) and fades out as it blends with the overlying condensed mesenchyme.

B) Stages 21 and 22. Only the most fibular fibers of PB attach to the base of the fifth metatarsal. The remainder of the fibers unite with the most fibular fibers of extensor digitorum longus (EDL).

C) Stage 23.
PB attaches fully to the base of M5 along with the most fibular fibers of EDL.



A

B

C

damage to the toes in the older specimens.

An interesting feature of extensor digitorum longus in the embryonic foot was that it presented as a broad, attenuated aponeurosis in the dorsum of the foot (Fig 42A and B). As this aponeurosis coursed towards the toes, four individual tendons became progressively more discrete and the fascia-like tissue webbed between the tendons became progressively less distinct (Fig 39C). This finding suggested that a common mesenchymal layer gave rise to both the extensor tendons and the deep fascia, differentiating from each other in a distoproximal fashion.

The most striking observation of extensor digitorum longus, which was previously mentioned, was the apparent union of the most fibular fibers from the aponeurotic sheet with the fibers of peroneus brevis and their conjoined attachment to the base of the fifth metatarsal (Fig 43C). In the adult foot, the tendon of extensor digitorum longus to the fifth digit demonstrated no attachment to peroneus brevis. However, a conjoined attachment of peroneus tertius and brevis to the base of the fifth metatarsal was observed (Fig 44). Therefore, a comparison of the adult and embryonic specimens suggested that the most fibular fibers of extensor digitorum longus aponeurotic expansion in the dorsum of the foot represented the tendon of peroneus tertius, but as yet unseparated from the extensor digitorum longus.

Fig 44. The course and distal attachments of the adult extensor and peroneal tendons of the right foot.

A) Dorsal view showing extensor digitorum longus (EDL) and the separate tendon of peroneus tertius (PT). Also shown are extensor hallucis longus (EHL) and peroneus brevis (PB).

B) Fibular view showing the distal attachments of peroneus brevis and tertius to the base of the fifth metatarsal. Also shown are the extensor digitorum brevis (edb) and the inferior limb of the extensor retinaculum (er) emerging from the tarsal sinus (arrow).

C) Enlarged detail of B showing the conjoined distal attachment of PB and PT. Also shown is an accessory tendon slip (arrow) from EDL to the shaft of the fifth metatarsal (M5).

A
EDL
PB
PT
EHL
B
er
edb
PB
C
PB
M5

In summary, examination of the extrinsic tendons found that:

1. the precise termination of embryonic tendons coursing into the toes was indistinct in the younger specimens due to the blastemal condition of the middle and distal phalanges
2. the long flexor and extensor tendons of the toes and tibialis anterior demonstrated undulations in their course through the embryonic foot
3. the adult calcaneal tendon and tibialis anterior tendon demonstrated torsion of their fibers
4. the termination of the embryonic tibialis posterior was virtually the same as the adult situation
5. the tendon-and-sheath unit of the embryonic peroneus longus appeared to mature, coalesce or migrate from the fibular towards the tibial side of the foot, gaining attachments to the neighbouring bones along the way; its distal attachment was only to the long, extended process of the base of the first metatarsal; additional attachment to the first cuneiform, as in the adult foot was not seen in any of the embryos
6. the embryonic peroneus brevis tendon gained increasing attachment to the base of the fifth metatarsal during stages 20 to 23; in five of the six embryos, it joined with the fibular most fibers of the attenuated tendon of extensor digitorum longus
7. a common mesenchymal layer seemed to give rise to both

the tendons of extensor digitorum longus and the deep fascia of the dorsum of the foot

8. the tendon of peroneus tertius was as yet unseparated from the tendon of extensor digitorum longus by the end of the embryonic period; it appeared to be represented by the most fibular fibers of the aponeurotic extensor digitorum longus which attached with peroneus brevis to the base of the fifth metatarsal

D. THE INTRINSIC MUSCLES

Whereas the previous section dealing with the extrinsic muscles focused on the distal attachments of their tendons, the particular emphasis of this section is on the intrinsic muscles attached to the calcaneus and those acting on the great toe.

Extensor digitorum brevis, as the only intrinsic muscle to arise in the dorsum of the foot, will be dealt with first. Like its adult counterpart, the embryonic muscle attached proximally to the anterior process of the calcaneus and the cervical ligament (Fig 45). However, unlike the adult foot where this attachment site was largely obscured by the overlying talus (Fig 46), the embryonic site of attachment was very exposed. Furthermore, in relation to the talus, the proximal portion of the muscle belly appeared to be situated on the fibular side of the hindfoot (Figs 37B and 45A). These findings were further evidence that the calcaneus was inverted below the talus.

Perhaps the most interesting of the intrinsic muscles were those of the first muscle layer in the sole. Of the three muscles in this layer, only the muscle belly of abductor digiti minimi attached proximally to the calcaneal tuberosity (Fig 48). The muscle bellies of flexor digitorum brevis and abductor hallucis did not extend as far proximally as the calcaneal tuberosity. As in the adult foot (Fig 47), the abductor digiti minimi attached proximally to the fibular side of the calcaneal tuberosity (Fig 48). In

Fig 45. The embryonic extensor digitorum brevis (drawn from transparency reconstructions.

The muscle arises from the anterior process of the calcaneus and the cervical ligament. This attachment site is exposed. A) Embryo XXI, right foot, anterofibular view.
The proximal portion of extensor digitorum brevis (edb) appears to be situated on the fibular side of the calcaneus. Also shown are the tendons of flexor digitorum longus (FDL) and flexor hallucis longus (FHL) coursing under the sustentaculum tali.

B) Embryo XXIIa, right foot, dorsal view.

C) Embryo XXIII, left foot, dorsal view.

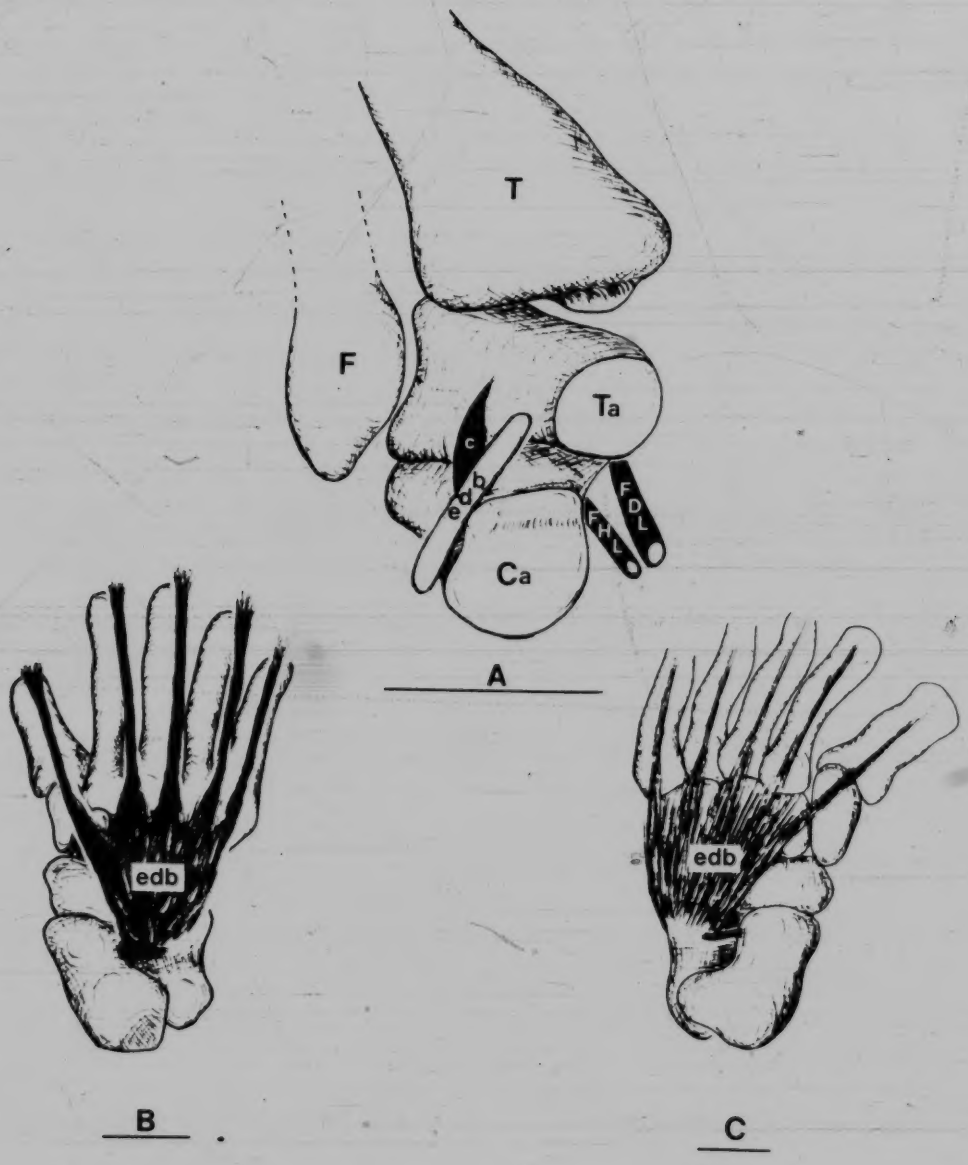
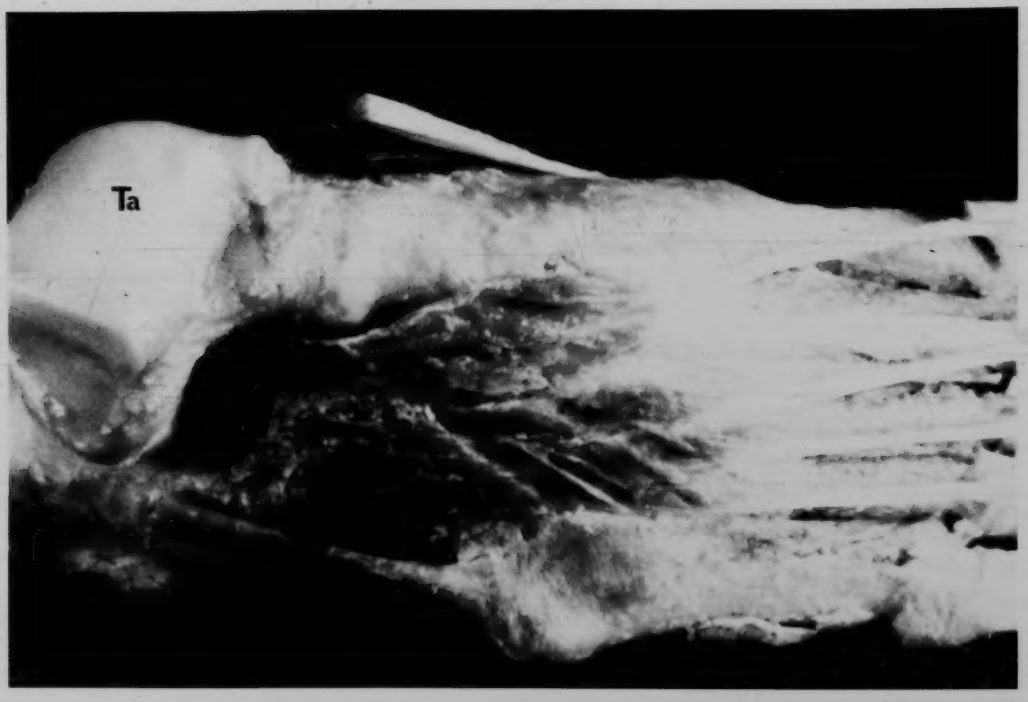

T
F
Ta
c
b
d
e
FDL
FHL
Ca
A
edb
B
edb
C

Fig 46. The adult extensor digitorum brevis (right foot).

Observe the proximal attachment of extensor digitorum brevis (edb) to the calcaneal sulcus. The more medial muscle fibers are obscured by the overlying talus (Ta). Also shown is the attachment of the inferior limb of the extensor retinaculum (arrow) deep in the tarsal sinus.

Fig 47. The adult abductor digiti minimi.

Observe the proximal attachment of abductor digiti minimi (abdm) to the calcaneus and the distal attachment of a lateral group to fibers to the base of the fifth metatarsal (M5). The remainder of the fibers terminate on the base of the proximal phalanx of the fifth toe (not shown).


Ta

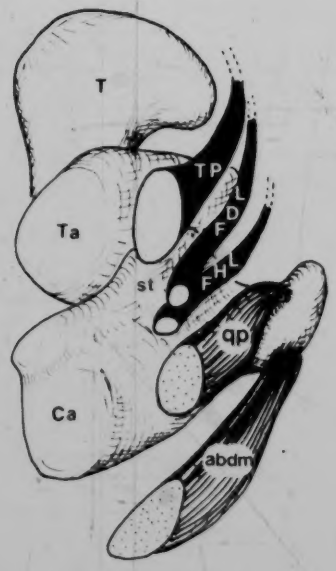
PT
PB
M5

Fig 48. The embryonic plantar intrinsic muscles (drawn from the transparency reconstructions).

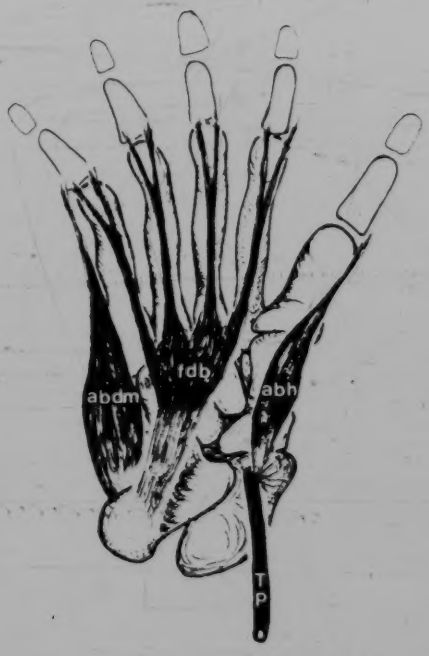
A) Embryo XXI, right hindfoot, anterotibial view. The proximal attachments of abductor digiti minimi (abdm) and quadratus plantae (qp) to the calcaneus (Ca) are shown. The muscle bellies of abductor hallucis (abh) and flexor digitorum brevis (fdb) do not extend into this hindfoot region.

B) Embryo XXIIa, right foot, plantar view.
Abdm is the only one of the three muscle bellies to attach directly to the calcaneus as seen in the adult foot.
The muscle belly of fdb extends proximally to the level of the calcaneocuboid joint. A thin mesenchymal condensation projects backward from fdb to attach to the calcaneus. Distally, its four tendons bifurcate to allow the passage of the tendons of flexor digitorum longus (not shown).
Abh fades out in the region of the sustentaculum tali where it blends with some of the fibers of tibialis posterior (TP) tendon.

C) Embryo XXIII, left foot, plantar view.
Only the proximal portions of the three muscles have been represented. As in A), only abdm attaches to the calcaneus.



A



B

C

the stage 20 embryos, the proximal extent of the muscle emerged from the precartilaginous calcaneal tuberosity. Distally it faded out in the region of the base of the fifth metatarsal. In three of the older specimens (XXI, XXIIb and XXIII) the muscle made an intermediate attachment to the base of the fifth metatarsal before proceeding into the fifth toe. In embryo XXIIa, attachment to the base of the fifth metatarsal was not apparent. The dissected adult limb demonstrated a similar intermediate attachment before terminating on the proximal phalanx of the fifth toe (Fig 47).

The muscle belly of abductor hallucis was well defined in the midfoot of the embryos and distally it fused with the tibial head of flexor hallucis brevis (Fig 35A), as in the adult foot. However, more proximally it seemed to fade out in the region of the sustentaculum tali. At higher magnification, the serial sections revealed that the muscle blended with the radiating fibers of tibialis posterior (see Figs 37C and D and 48B). This feature contrasted sharply to the adult situation in which abductor hallucis attached directly to the tibial side of the calcaneal tuberosity (Fig 49A).

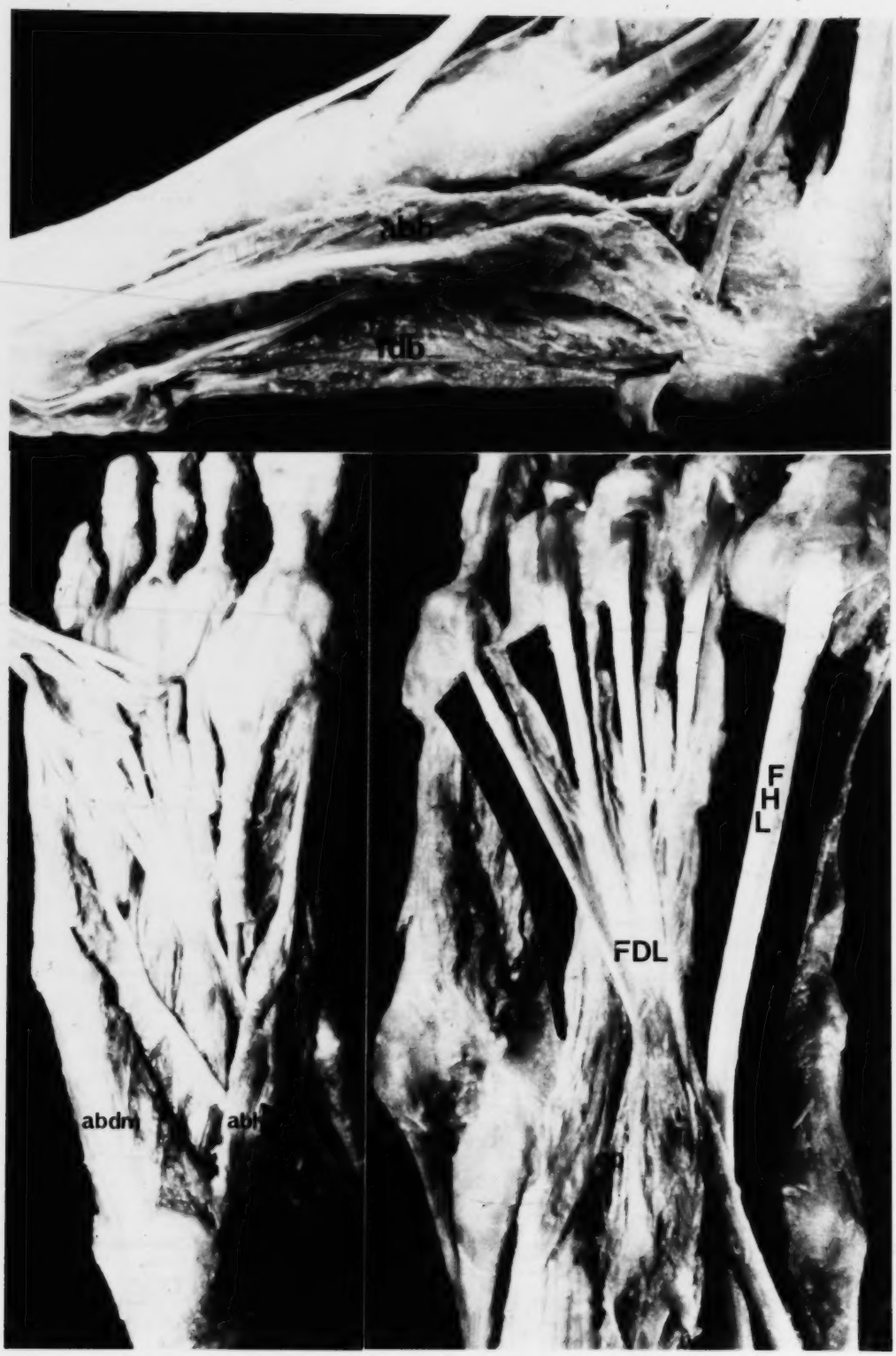
Similarly, the muscle belly of the embryonic flexor digitorum brevis did not attach to the calcaneal tuberosity as the adult limb showed (Figs 48 and 49A). At stage 20, it extended proximally to the naviculocuneiform interzone. By stage 23 the muscle had extended proximally to the level of

Fig 49. The adult intrinsic muscles of the first and second layers of the sole.

A). Medial view showing the proximal attachment of abductor hallucis (abh) to the calcaneus and the distal attachment to the proximal phalanx of the first toes. Also shown is flexor digitorum brevis (fdb).

B) Plantar view with fdb reflected to show abductor digiti minimi (abdm) and abh attaching proximally to the calcaneus.

C). Plantar view of the intrinsic muscles of the second layer of the sole and related extrinsic tendons. The two heads of quadratus plantae (qp) attach proximally to the medial side of the calcaneus and the long plantar ligament. Distally, the muscle fuses with flexor digitorum longus (FDL). Also shown are the four lumbricals (l) arising from the tendons of FDL.


A
fdb
B
abdm
abl
C
FDL
F
H
L

the talonavicular joint which suggested that the muscle had grown in length toward the calcaneus over the series examined. At all stages, it was proportionately smaller than the adult condition as well as being smaller than the quadratus plantae of the same specimen. The relative sizes of the embryonic flexor digitorum brevis and quadratus plantae are shown in figure 50.

The sagittal sections of embryo XXIIb showed that the proximal portion of the fleshy belly of flexor digitorum brevis was continuous with a thin mesenchymal condensation that projected backwards and attached with the plantar aponeurosis to the calcaneal tuberosity (Fig 50). The transparency model of embryo XXIIa also demonstrated a backwards projecting band of tissue which appeared to connect to the calcaneal tuberosity; however it was not possible to distinquish a strand of tissue separate from the plantar aponeurosis. Distally, four tendons emerged from the muscle belly, bifurcated in the region of the metatarsophalangeal joints and then coursed into the toes (Figs 35A and 48B).

Throughout the embryonic series, the quadratus plantae was observed attaching proximally to the calcaneus and distally to flexor digitorum longus and flexor hallucis longus (Fig 33C and Dand 35A). In embryo XXIII (Fig 33D), both the tibial and fibular heads were apparent, as in the adult foot (Fig 49C). However, in all the younger specimens, only one head was discerned which arose from the concavity

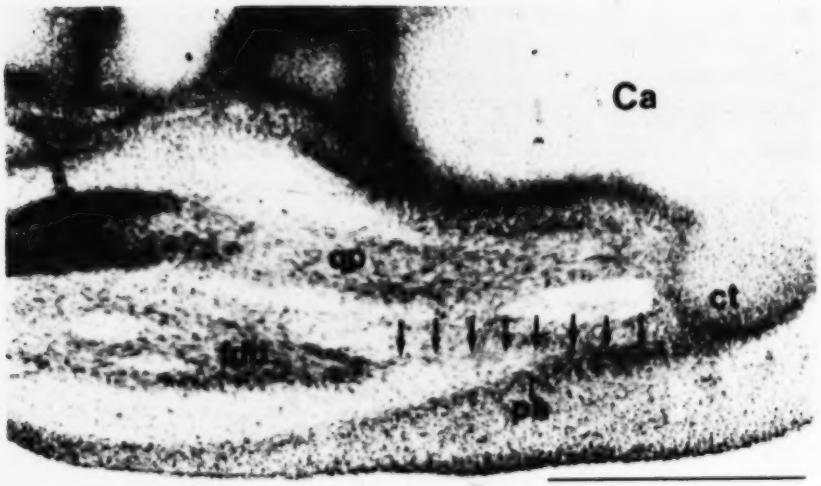
Fig 50. Photomicrograph of a sagittal section through the right foot of embryo XXIIb, demonstrating flexor digitorum brevis.

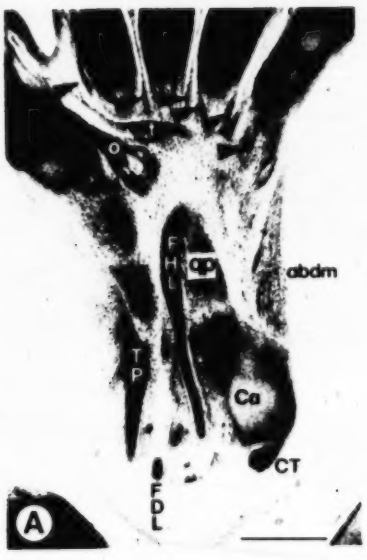
A band of tissue (broken line) extends proximally from the muscle belly of flexor digitorum brevis (fdb) to attach with the plantar aponeurosis (dotted line) to the calcaneus (arrow).

Fig 51. The interossei and adductor hallucis in embryo XXIIa.

A) Photomicrograph of a horizontal section through the right foot viewed from above, demonstrating adductor hallucis and the interossei (arrows) Histologically, the transverse head (t) of adductor hallucis appears to be more developed than the oblique head (o).

B) Drawn from the transparency reconstruction, viewed from below. The seven interossei (i) arise from the shafts of the metatarsals and course into the toes. At this stage, their termination





B

on the tibial side of the calcaneus and the long plantar ligament. This finding suggested that up to stage 22, the muscle existed as a single mass that had not yet differentiated into two distinct heads.

The distinquishing feature about the embryonic adductor hallucis was that histologically, its transverse head appeared to be less developed than its oblique head. This characteristic was readily apparent from the horizontal sections of embryo XXIIa (Fig 51a). Figure 51b shows the two heads of the adductor hallucis as well as the seven interossei which are arranged as in the adult foot.

In summary, examination of the embryonic intrinsic muscles found that:

1. the proximal attachment site of extensor digitorum brevis was exposed much more than the adult condition, possibly due to the inverted (laterally rotated) position of the calcaneus,
2. of the three muscles in the first layer of the sole, only the muscle belly of abductor digiti minimi attached proximally to the calcaneus,
3. the proximal extent of abductor hallucis faded out in the region of the sustentaculum tali, blending with the diffuse fibers of the posterior tibial tendon,
4. the muscle belly of flexor digitorum brevis extended proximally to the region of the calcaneocuboid joint; in the older embryos, a backwards projecting band of tissue appeared to attach with the plantar aponeurosis to the calcaneal tuberosity,
5. the transverse head of the adductor hallucis seemed to be differentiated less than the oblique head,
6. the quadratus plantae existed as a single muscle mass which did not differentiate into two distinct heads until stage 23,
7. the lumbricals and interossei appeared to be identical in proportion and size and arrangement to the adult condition.

V. DISCUSSION

The literature review demonstrated great discrepancy with respect to relationships of the skeletal elements of the embryonic foot. A general lack of information pertaining to the relationships and attachments of muscles in the embryonic foot was also evident.

The present study focused on the size, shape and relationships of the musculoskeletal elements of the human embryonic foot with the following objectives:

1. to identify the factors that may be responsible for the posture of the embryonic foot
2. to compare the characteristics of the musculoskeletal elements in the embryonic foot with the pathonatomical features of various congenital foot anomalies.

A. DISCUSSION OF MATERIALS AND METHODS

The human foot possesses unique qualities (e.g. the well-developed medial longitudinal arch) which distinquish it from all other animals (Jones, 1949). Therefore, human material was used rather than an animal model. Since fresh human material could not be obtained, the resources of the Shaner Collection were used. Unfortunately, this embryonic material had been processed to study development in the thoracic region and imposed several limitations on this study. Only six specimens in the collection were suitable for this study. Since all six were abortuses, and the medical history was either limited or not recorded, there was no assurance that the selected specimens were representative of typical embryonic development. Furthermore, the external appearance recorded prior to sectioning for four of the specimens provided only limited information concerning the posture of the lower limbs and there was no assurance that the intrauterine limb position had been preserved accurately. However, there was no reason to suspect that the specimens were abnormal in any way and have been used by previous workers as representative of normal (Zaw-Tun, 1982 and 1985; Wilson, 1983). Finally, the absence of a system of external reference markers required that the method of "best fit" be used in aligning the serial tracings. Despite these limitations, the use of a limited number of human specimens was considered distinctly superior to using an animal model, where the number of specimens

could have been more numerous. Considering that the human foot is unique (Jones, 1949), it is questionable whether an animal model can represent adequately its prenatal development.

Although there is always some degree of doubt when serial tracings are aligned without external markers (Ware and LoPresti, 1975; Guant and Guant, 1978), the method of best fit is an accepted and recognized scientific technique that continues to be used by other workers (Levinthal and Ware, 1977; Zaw-Tun, 1982 and 1985; Wilson, 1983). The accuracy of alignment is maximized by using at least six reference contours (Gaunt and Gaunt, 1978). In this study, a minimum of 15 contours was included in each tracing, ensuring a high degree of validity.

It was often difficult to compare directly the findings from this study with previous investigations. A fundamental problem centred on the age of the embryos which was determined by one of two methods: CRL or staging. The majority of investigators who have studied the prenatal development of the foot have used CRL (Bardeen and Lewis, 1901; Bardeen, 1905; Bohm, 1929; Jones, 1949; Olivier, 1962; Martinez-Cuadrado and Gonzalez-Santander, 1967; Cihak, 1972; Victoria-Diaz and Victoria-Diaz, 1984). However, Bagnall *et al.* (1975) advised against regarding CRL as a precise indication of gestational age due to the variable flexion of embryos. In contrast, Streeter's (1948 and 1951) method of staging embryos, appeared to be more reliable than CRL as an

indication of relative maturity. Furthermore, this method was particularly well-suited to this study because O'Rahilly *et al.* (1957) has defined more precise criteria for each stage, related specifically to chondrification in the foot. Consequently, the relative maturity of each embryo in this study was defined in terms of its stage of development according to a system of aging developed by Streeter (1948 and 1951) and refined by O'Rahilly *et al.* (1957) (see Table 1). Unfortunately, this system has only been used in a few studies which have had access to the Carnegie collection (O'Rahilly, 1953, 1957, 1973; O'Rahilly and Gardner, 1975; O'Rahilly *et al.*, 1956, 1957; Gardner *et al.*, 1959). As a result, direct comparison of the results with embryos of similar maturity from other studies was often difficult.

Previous investigators of the embryonic development of the human foot have used either serial section analysis (Leboucq, 1882, cited in Jones, 1949; Jones, 1949; O'Rahilly, 1953, 1957, 1973; O'Rahilly and Gardner, 1975; O'Rahilly *et al.*, 1956, 1957; Gardner *et al.*, 1959; Cihak, 1972; Victoria-Diaz and Victoria-Diaz, 1984) or three-dimensional serial reconstructions (Schomburg, 1900, cited in Bohm, 1929; Bardeen and Lewis, 1901; Bardeen, 1905; Straus, 1927; Bohm, 1929; Olivier, 1962; Martinez-Cuadrado and Gonzalez-Santander, 1967; Huson, 1969).

The primary tool of investigation utilized in this study was three-dimensional reconstruction which O'Rahilly (1973) considered to be optimal for the investigation of

embryonic foot development. Serial section analysis was also used, but to a lesser extent. As a result of using both methods, the various attributes of each became apparent. It was found that spatial relationships could be appreciated better from serial reconstructions than from serial sections alone. This became apparent when, only the skeletal elements of embryo XXIIa were reconstructed as a wax model and interpretation of the muscular structures was attempted from the serial sections alone. When this same specimen was later reconstructed as a transparency reconstruction, depicting both the muscular and skeletal elements, the spatial relationships were readily apparent. Indeed, many of these relationships differed from those interpreted solely from the serial sections. These discrepancies emphasized the importance of visualizing the internal structures in relationship to each other in three dimensions. Another distinct advantage of reconstruction over serial section analysis was the ability to measure the skeletal elements from the transparency models. Finally, it was possible to present the internal structures in dimensionally-accurate illustrations which were developed from photographs of the transparency reconstructions (see Fig 12). In contrast, the production of illustrations based on the observations from serial section analysis would not have been dimensionally-accurate. Therefore, it was concluded that although transparency reconstruction proved to be an arduous and time consuming task, the information gained from the

three-dimensional presentation of spatial relationships justified the effort.

The merit of Verbout's (1985) recommendation to analyze sections from all three planes also became evident. When the skeletal relationships in the hindfoot were interpreted from reconstructions of the sagittally-sectioned (XXa) and the horizontally-sectioned (XXIIa and XXIII) embryos, the embryonic condition and the future adult configuration seemed to be strikingly different. For example, the embryonic calcaneus appeared to be situated on the fibular side of the talus rather than below it as seen in the adult foot. Furthermore, these preliminary findings were substantiated by much of the literature (Bardeen, 1905; Bohm, 1929; Martinez-Cuadrado and Gonzalez-Santander, 1967; Victoria-Diaz and Victoria-Diaz, 1984). However, the reconstruction of the coronally-sectioned embryo XXI clearly indicated that the talus was superimposed on the calcaneus, as in the adult, thereby refuting the findings of other workers and demonstrating how the plane of section can lead to erroneus interpretation of spatial relationships. Moreover, the ability to visualize the internal features varied with each of the three sectional planes. For example, the longitudinal arching of the embryonic skeletal elements was more apparent from the sagittal sections than the other two sectional planes. In contrast, the course of the peroneus longus tendon across the sole of the foot was more difficult to interpret from sagittal sections, where it was

cut in cross section, than either of the other two sectional planes where it was cut longitudinally.

Although it was not possible to represent all four stages of development with specimens in each of the three planes of section, each stage was represented by a separate reconstruction. Of the four transparency models, one was developed from sagittal sections (embryo XXa), one from coronal sections (embryo XXI) and two from horizontal sections (embryo XXIIa and XXIII). Therefore, the period of development studied (i.e. stages 20 through 23) was represented by reconstructions in each of the three sectional planes.

As previously indicated, this study used both wax-plate and transparency reconstructions. Both were equally time-consuming and laborious to construct. The major advantage of transparency reconstruction was that all the internal structures of the foot could be represented in a single model. In contrast, it was not possible to represent skeletal and muscular tissues in a single wax-plate model because the skeletal elements would be almost entirely obscured by the overlying musculotendinous structures. After constructing the skeletal elements of the embryo XXIIa, it was concluded that the wax-plate method was not well-suited to the study of such disconnected structures. The intricate wire bridges that were required to retain the shape and relationships of the individual bones, detracted greatly from the ease of construction and made the model extremely

delicate. However, when compared to the transparency reconstruction, it was easier to interpret the skeletal relationships from the wax model because it could be viewed from any angle. With the transparency model, the view was restricted to the full face view (i.e. perpendicular to the surface of the acetate sheets) and a limited range of oblique views.

Whereas the process of producing the wax contours required that the contours first be drawn onto paper, then traced onto the wax and finally cut from the wax (i.e. a three step process), the contours for the transparency reconstruction could be produced directly onto the acetate sheets in one step. Since each reproduction of the contours introduces more error into the reconstruction, wax models are less accurate than the transparency reconstructions. However, this disadvantage was offset by the ease with which descriptive photographs of the wax model could be taken directly. In contrast, to provide a comprehensible image of the transparency reconstructions, it was necessary to produce line drawings from the photographs of the models.

It is recognized that the methods used in this study were less than optimal. If the resources had been available, the ideal methodology would have utilized fresh human embryos, ensuring that only those without obvious external deformity were used. The intact specimens would have been photographed from various angles (anterior, lateral, superior and inferior views) prior to sectioning, while

ensuring that the intrauterine posture of the lower limb was not disturbed. The limb would have been removed and embedded in glycol methacrylate with the inclusion of external reference markers. Current histological techniques would ensure optimal histological quality: methacrylate permitting thin serial sections, enhancing the visualization of the histology as well as preserving the internal arrangement of the tissues. The limb would have been sectioned in precisely the plane desired, avoiding section obliquity. Each stage of development would have been represented by a minimum of three specimens so that each of the three sectional planes could have been analyzed. Specimens younger than stage 20 would have been examined, using serial section analysis alone, to examine the musculoskeletal relationships during the earlier stages of embryonic development. These earlier specimens would probably not lend themselves to serial reconstruction because the skeletal elements would not be chondrified sufficiently to identify their boundaries. Finally, computergraphics would have been utilized to facilitate the reconstruction procedure and measuring and to eliminate the need to convert the information contained in the three-dimensional reconstructions into a two-dimensional illustration for publication. While this proposed methodology would have been optimal, it is not anticipated that it would yield different results. The consistency of the findings from the six specimens examined is a good indication of their validity.

B. DISCUSSION OF RESULTS

The results of this study describe the postures of the human foot as well as the size, shape and relationships of the musculoskeletal elements during stages 20 through 23 of the embryonic period, identifying developmental trends and comparing the embryonic features with the adult condition.

A review of the literature found only eight studies that have used serial reconstructions to investigate the prenatal development of the foot. All eight employed solid reconstruction techniques, similar to the wax-plate method used in this study. Seven of these studies were based on reconstructions of only the skeletal elements of the prenatal lower limb (Schomburg, 1900, cited in Bohm, 1929; Bardeen, 1905; Straus, 1927; Bohm, 1929; Martinex Cuadrado and Gonzalez-Santander, 1967; Huson, 1969). Only the study by Bardeen and Lewis (1901) reconstructed all the internal structures of the lower limb. However, they were concerned with the progressive maturation of the internal elements rather than their arrangement. Their reconstructions resembled a superficial dissection and the musculoskeletal relationships were neither apparent from the drawings nor described. In contrast to all previous investigations, the present study is unique both in its utilization of transparency reconstruction and in providing the first detailed analysis of the musculoskeletal relationships in the human embryonic foot.

Skeletal Maturity and Variations

The most significant finding concerning skeletal maturation over stages 20 through 23 was thought to be the pattern of proximodistal chondrification of the phalanges, commencing after the tarsal and metatarsal elements had chondrified. This sequence of chondrification agrees with the findings of Senior (1929) and O'Rahilly *et al.* (1957). This might have a bearing on muscle function as it is conceivable that the distal attachment of the long flexor and extensor tendons is less secure and that muscle contraction is less effective when the phalanges are represented by condensed mesenchyme than when they are chondrified. If a chondrified skeletal element does indeed provide a more secure attachment than a mesenchymal element, then it would seem that these tendons could not be firmly anchored distally until stage 23, when the middle and distal phalanges, in addition to the proximal phalanges, were chondrified. Unfortunately, there was no way to assess the relative strength of the tendon attachments in these specimens and previous investigators have not addressed this issue.

Very few skeletal variations were detected in this study and were confined to accessory ossicles in four of the six specimens (Figs 20 and 36). The most striking of these was the cartilaginous projection from the posterior part of the sustentaculum tali in embryo XXIII (Fig 24C). Its appearance suggested that it was the os sustentaculi, an

accessory ossicle described by Dwight (1907), Jones (1949) and O'Rahilly (1957). According to these workers, the ossicle is usually partly fused with the sustentaculum tali (as seen in embryo XXIII). Based on its location, the ossicle in embryo XXI (Fig 20A) was identified as the os intermetatarseum that has been described by Jones (1949), O'Rahilly (1957), Cihak (1972) and Mann (1978). According to Cihak (1972), the os intermetatarseum is a constant structure seen in the embryonic foot and usually disappears after 30mm CRL (i.e. about stage 23). He concluded that this ossicle bears the characteristic of an atavistic structure recapitulated during ontogeny. In contrast, neither Jones (1949) nor O'Rahilly (1957) regarded accessory ossicles as being atavistic elements. The ossicle found in embryo XXIIb (Fig 20B) was considered to be the os cuneometatarsale described by O'Rahilly (1957). In embryos XXIIa and XXIII, a mesenchymal condensation was detected deep to the talar head to which the tendon of tibialis posterior was attached (Figs 36A, B, and C). This condensation was thought to represent either the sesamoid bone developing in the tendon of tibialis posterior, which is found in approximately 23% of the population (Anderson, 1983), or the accessory navicular (i.e. os tibiale externum) which occurs in about 4% of the population (Anderson, 1983). O'Rahilly (1957) regarded accessory ossicles in general, as common occurrences in otherwise normally-developing feet. Therefore, it would seem that these ossicles represent minor skeletal variations

(being commonly found by other investigators) and probably have little effect, if any on the development of the embryonic foot.

Skeletal Relationships in the Hindfoot

The most striking contrast between the findings from this study and the documentation of others pertained to the skeletal relationships in the hindfoot. The present study found that at least as early as stage 20 (approximately 20mm CRL), the relationships in the embryonic hindfoot were similar to the adult condition:

1. the calcaneus was situated **below** the talus
2. the **fibula projected further** distally than the tibia
3. there was no evidence that the tip of the fibular malleolus was in contact with the calcaneus during stages 20 through 23

In contrast, much of the previous literature reported that initially:

1. the calcaneus is situated **on the fibular side** of the talus (Bardeen, 1905; Bohm, 1929; Martinez-Cuadrado and Gonzalez-Santander, 1967; Victoria-Diaz and Victoria-Diaz, 1984)
2. the **tibia projects further** distally than the fibula (Bardeen, 1905; Straus, 1927; Jones, 1949; Victoria Diaz and Victoria-Diaz, 1984)
3. the **fibula rests upon the calcaneus** (Hagen, 1900, cited in Jones, 1949; Schomburg, 1900, cited in Bardeen, 1905; Jones, 1949).

Only Schomburg (1900, cited in Bardeen, 1905) reported that from the outset, the talus is situated above the calcaneus.

There are two possible explanations that might account for the discrepancies between this study and most of the previous documentation. Skeletal development at stage 20 may already be too advanced to capture the embryonic relationships reported by other workers. Some studied specimens smaller than 20mm CRL, which is approximately the length of a stage 20 embryo. However, it is also possible that these workers were not reporting a real difference in the skeletal arrangement, but rather interpreted the information differently. When the reconstructions from the present study (Figs 23 and 24) are compared to those produced by other workers (Fig 52) it is readily apparent that there is no difference in the arrangement of the skeletal elements. In particular, they all appear to show that the calcaneus is situated on the fibular side of the talus. Similarly, when the horizontal sections from the present study (Fig 25) are compared with horizontal sections published by Bardeen (1905) and Jones (1949) (Fig 53), this unusual talocalcaneal relationship is suggested again. It might also be interpreted from these sections, as well as from the posterior view of the wax model (Fig 26A), that the tibia extends further than the fibula. However, it must be appreciated that all these interpretations are based on the assumption that the embryonic forefoot is directed downward, as in the anatomical position. What is not readily apparent from these figures is the marked forefoot inversion, a feature clearly demonstrated only in the reconstruction of

Fig 52. Three-dimensional reconstructions by previous workers.

A) Wax-plate reconstruction of 23mm embryo reconstructed by Bohm (1929).

B) Reconstructions by Olivier (1962).

C) Reconstructions by Martinez-Cuadrado and Gonzalez-Santander (1969)

Fig 52 has been removed because of the unavailability of copyright permission.

Fig 53 was removed because of the unavailability of copyright permission. It contained horizontal sections published by pervious workers.

A) Horizontal section from first half of the second month (Bardeen, 1901)

B) Projection drawing of horizontal section from an 18mm embryo (Jones, 1949)

the coronally-sectioned embryo XXI. When the forefoot inversion is taken into account, and the hindfoot elements are examined from coronal sections, or reconstructions based on coronal sections (see Figs 26 and 27), it is clearly apparent that the embryonic calcaneus is situated below the talus and that the fibula extends further than the tibia, as in the adult foot. Therefore, the findings from this study showed that by at least stage 20, the arrangement of the skeletal elements in the hindfoot was actually very similar to the adult condition. Rather, it was the inverted position of the embryonic forefoot that was the striking contrast. The majority of other workers have focused their attention on the apparent hindfoot arrangement, without recognizing or considering the posture of the forefoot. Therefore, the discrepancy between the findings from the present study and earlier investigations does not indicate a real difference in the arrangement of the skeletal elements, but rather that the information was interpreted differently. Consequently, there was no evidence from this study to support the theory of Victoria-Diaz and Victoria-Diaz (1984) that a growth spurt of the distal end of the fibula, occurring from 20 to 30mm CRL, pushes the calcaneus beneath the talus. These workers did not actually measure the relative lengths of the tibia and fibula; their conclusions were based solely on observations from serial sections. Also, it should be noted that many of their specimens up to 26mm CRL were sectioned obliquely and none of these smaller embryos were sectioned

in the coronal plane. To determine whether the skeletal relationships reported in previous studies are representative of younger embryos, it would be necessary to look at coronally-sectioned feet from specimens earlier than stage 20. Clarification of these early relationships is essential to the understanding of the ontogeny of the foot.

Shape and Proportionate Size of Skeletal Elements

The results clearly showed that in the embryonic foot, the shape and proportionate size of the calcaneus and first metatarsal differed sharply from the adult foot. The embryonic talus also differed from its adult counterpart but only with respect to its shape. The shape and proportionate size of the other embryonic skeletal elements were not obviously different from the adult condition.

Calcaneus: At all four embryonic stages, the calcaneus was found to be proportionately shorter in relation to the talus than the adult condition (see Figs 23 and 24). This observation agreed with the reports by Straus (1927), Keith (1929) and Schultz (1930). The difference in the contours of the embryonic and adult calcanei depicted in figure 28 suggested that the articular facet for the cuboid and the anterior process of the embryonic calcaneus, would have to be remodelled to achieve the shape of the adult bone. Similarly, figure 26 drew attention to the marked inversion of the embryonic calcaneal tuberosity. Although this was attributed in part to the inverted position of the calcaneus in relation to the talus, it was strongly suggested that the long axis of the calcaneal tuberosity was concavely bowed toward the sustentaculum tali. It was concluded that after the embryonic period, both remodelling and differential growth of the calcaneus would be required to attain its adult shape and proportions. In support, Jones (1949) stated that the outstanding ontogenetic change in the calcaneus was

its growth relative to the total foot length. However, ontogenetic remodelling of the calcaneus was not previously reported.

First Metatarsal: The first metatarsal was found to be proportionately shorter in relation to the second metatarsal than the adult condition, in accordance with the findings of other workers (Keith, 1929; Schultz, 1930; and Morton, 1942). Whereas the adult first metatarsal was 83% as long as the second metatarsal, in embryo XXIIa it was only 50% as long, while in embryo XXIII it was 69% as long as the second. The difference between stages 22 and 23, where the first metatarsal had dramatically increased its length by 34%, was a striking example of disproportionate growth during the ontogeny of the foot. Straus (1927) also observed an ontogenetic increase in the relative length of the first metatarsal, reporting values of 69.9% (almost identical to embryo XXIII) at eight weeks gestation and 74.9% at three months.

Other interesting features of the embryonic first metatarsal included the long process at the attachment of the peroneus longus and the distinctly concave proximal articular surface which corresponded to the convex surface on the first cuneiform. In the adult, no such process was seen and the first cuneiometatarsal joint was flat. Although Jones (1949) insisted that the embryonic first cuneiometatarsal joint is always flat, a previous, apparently more extensive study by Straus (1927) found

several older human fetuses possessing definite rounding of the first cuneiform. As with the calcaneus, the contrast between the embryonic and adult feet suggested that during its ontogeny, the first metatarsal is subjected to both differential growth and remodelling to attain its adult proportion and shape.

Talus: The most striking difference between the embryonic and adult tali was the apparent lack of torsion or constriction of the embryonic talar neck. Associated with this was the observation that the long axis of the talar head was oriented horizontally in the embryo, while in the adult this axis was oblique (see Figs 28 and 30A). According to Straus (1927), the long axis of the talar head undergoes a rotation during ontogeny due to torsion of the talar neck. He reported that the angle between this long axis and the trochlear surface of the talus was less than 20° in the midterm fetus and about 40 degrees in the adult. Therefore, the findings from this study and the work by Straus (1927) strongly suggest that the talus is remodelled during its ontogeny. The factors that may contribute to this remodelling will be considered later.

The Postures of the Embryonic Foot

The most striking contrasts between the embryonic and anatomical positions of the foot as seen in the adult foot included:

1. lateral rotation of the limb as a whole
2. extreme plantar flexion at the ankle (measured as 62° from the reconstruction of embryo XXa) (see Fig 9K)
3. adduction of the foot toward the tibia (see Figs 1, 17 and 18)

These observations, which were readily apparent from the external form of the lower limb (observed from the reconstructions and the serial sections), concurred with the findings of others (Schomburg, 1900; Bardeen, 1905; Bohm, 1929: Streeter, 1951; O'Rahilly and Gardner, 1975; Victoria-Diaz and Victoria-Diaz, 1984).

When the arrangement and orientation of the skeletal elements were analyzed from the reconstructions, the following additional observations were made:

1. calcaneal inversion
2. forefoot inversion
3. absence of the tibial longitudinal arch
4. hallucial divergence at stage 22 due to marked divergence of the first metatarsal
5. marked forefoot adduction at stage 23 due to bowing of the metatarsals toward the tibia

These five observations will now be discussed in more detail.

Calcaneal Inversion: Figures 26C, 26D and 28 demonstrate several features indicating that the embryonic calcaneus was inverted in relation to the talus when compared to the adult foot:

1. the upwards tilt of the sustentaculum tali
2. the marked inversion of the calcaneal tuberosity
3. the outward orientation of the calcaneal sulcus
4. the prominent cervical ligament

Inversion of the embryonic calcaneus was also described by Straus (1927) and Bohm (1929). The latter reported that in the reconstruction of a 35mm embryo, the dorsal surface of the calcaneus was tilted laterally (i.e. outward) due to marked "supination" of the bone in relation to the talus. According to MacConaill (1945), supination denotes a combination of inversion and adduction, while pronation represents a combination eversion and abduction. It is uncertain from Bohm's (1929) description whether or not the calcaneus was indeed adducted as well as inverted. Straus (1927) measured the angle between the long axis of the tibia and the long axis of the calcaneal tuberosity to determine the "torsion of the calcaneus which serves as an index for supination of the foot". He reported that the "torsion" reduces from about 37° in the three month fetus to about 3.5° in the adult. This measurement could not be made from the reconstruction of embryo XXI because the long axis of the calcaneal tuberosity appeared to be bowed (see Fig 26C). Straus (1949) also stated that reduction of the supination

is the most characteristic change of the fourth month of gestation and that it is not yet complete in the newborn.

Forefoot Inversion: Whereas in the adult foot the line intersecting the first and fifth metatarsal heads was perpendicular to the long axis of the leg, in embryo XXI the line was inverted 35° (see Figs 9L, 30A and 30B). This indicated marked inversion of the embryonic forefoot. Inversion of the prenatal forefoot was measured by only one other worker. Bohm (1929) reported that in the reconstructed lower limb of a 57mm embryo, the line through the metatarsal heads formed an angle of about 45° with the theoretical weight-bearing plane of the foot, which is similar to the measurement for embryo XXI.

It was further observed from the reconstruction of embryo XXI that the line intersecting the first and fifth metatarsals was approximately parallel to the sustentaculum tali, indicating that the forefoot and the calcaneus were both inverted to about the same extent. Therefore, it was concluded that the sole of the foot was supinated due to inversion at the subtalar joint; as in the adult foot, the talus and the ankle mortice represented one functional unit while the calcaneus in combination with the elements distal to the transverse tarsal joint comprised the other functional unit. According to Breathnach (1967), forefoot inversion persists until about age two or three. After this age, the definitive forefoot-hindfoot relationship develops where the forefoot is parallel to the floor and

perpendicular to the vertical axis of the calcaneus.

Absence of the Tibial Longitudinal Arch: The apparent absence of the embryonic tibial longitudinal arch, in the presence of a well-developed fibular longitudinal arch, was in sharp contrast to the adult foot where the tibial border was arched more than the fibular side (Fig 21). This embryonic feature, also reported by Bohm (1929), was attributed to the supinated (i.e. inverted and adducted) position of the embryonic forefoot. Associated with this feature was the apparent lack of torsion and constriction of the talar neck and the horizontal orientation of the long axis of the talar neck, which were previously discussed. Jones (1949) interpreted that the torsion of the talar neck occurs as the tibial margin of the forefoot is rotated downwards (pronated) during fetal and postnatal life to direct the sole toward the ground. It seems reasonable to suggest that as the forefoot is pronated, the arched configuration of the tibial side of the foot would be created.

Hallucial Divergence: Hallucial divergence of the embryonic foot was attributed to the convexity of the metatarsal surface of the first cuneiform (previously described) and the angle of abduction between the first and second metatarsals. This angle measured 19.5° in embryo XXIIa and 21.6° in embryo XXIII (Fig 23B). In contrast, the angle between the second and third metatarsals for embryos XXIIa and XXIII was found to be only 9° and 10.6°

respectively (see Table 3). Marked divergence of the first metatarsal was also reported by Leboucq (1882, cited in Straus, 1927), Bohm (1929), Schultz (1930) and Cihak (1972). Straus (1927) reported that the angle between the first and second metatarsals was 32° at eight weeks and 18.7° at three months.

Forefoot Adduction: Whereas embryo XXIIa demonstrated fan-spread digits with marked divergence of the hallux, in embryo XXIII the entire forefoot was adducted toward the tibia. This was largely due to the outer four metatarsals being concavely bowed toward the divergent first metatarsal (Fig 23). The effect was to give the foot a convex fibular border and a concave tibial border, similar to the shape of a congenital clubfoot.

According to Bohm (1929) and Keith (1929), adduction of the forefoot is characteristic of the early fetal period. Keith (1929) attributed this postural change to the movement of the outer four metatarsal heads towards the already adducted, static first metatarsal. The marked differential growth of the first metatarsal (described earlier), occurring during the later stages of embryo development, may also be a factor. It is possible that if the growth of the skeletal elements along the tibial side of the foot exceeds the growth of the soft tissues, then abductor hallucis might act like the string of a bow, causing the skeletal elements to be bowed between its proximal and distal attachments. The fact that a short abductor hallucis is sometimes implicated

in congentital metatarsus adductus and that surgical lengthening of the muscle reduces the deformity (Turco, 1981) lends support to this theory.

Biomechanical Considerations

The following section addresses those biomechanical factors which might account, at least in part, for the postural features of the embryonic foot. Since the biomechanical function of the embryonic foot has not been previously investigated, the basis of this discussion is dependent on those biomechanical principles that are known to apply to the adult foot.

Axes of Joint Rotation: Biomechanical studies of the adult foot have demonstrated that the inclination of the subtalar joint combines calcaneal inversion with adduction and plantar flexion of the foot as a whole (Manter, 1941; Hicks, 1953). Conversely, calcaneal eversion occurs with abduction and dorsiflexion. Similarly, the inclination of the ankle joint axis causes the foot to deviate medially (adduct) during plantar flexion and deviate laterally (abduct) in dorsiflexion (Inman, 1969). Although the axes of joint rotation in the embryonic foot have not been determined in this or other studies, it is entirely possible that the axes of the ankle and subtalar joints account in part for the combination of ankle plantar flexion, calcaneal inversion and adduction of the foot which are characteristic of stages 20 through 23.

Tendon-Axis Relationships: In the adult foot, posture and movement are influenced by the relative power of the individual muscles coupled with the relationships of the tendons to the joint axes. To understand the possible

contribution of muscular forces to joint alignment in the embyronic foot, it must be appreciated that tendon-axis relationships change through the range of motion of all joints (Jahss, 1982; Rose, 1982).

As in the adult foot, the only extrinsic musculature attaching to the calcaneus at all four stages were the calcaneal tendon (Fig 33) and the tendon of tibialis posterior (Fig 37). Turco (1981) pointed out that (at least postnatally) these structures function synergistically to simultaneously plantar flex the ankle and invert the calcaneus at the subtalar joint. In addition, when the heel is positioned in varus (as in the embryonic foot), the calcaneal tendon is situated further from the subtalar joint, thereby increasing its inversion power (Jahss, 1982). It was also observed in the reconstruction of embryo XXI, that the site of attachment of the calcaneal tendon appeared to extend higher on the tibial side (Fig 32A). This suggested that the triceps surae (gastrocnemius and soleus combined) might be exerting a greater upwards force on the tibial side of the calcaneal tendon due to the predominance of tendon fibers attaching to this area. This in turn would cause the calcaneus to invert while the ankle was being plantar flexed. Therefore, the same muscles that are causing plantar flexion in the embryonic foot also appear to be invertors of the calcaneus, showing that muscle function, in addition to joint axes, favours the combination of plantar flexion and calcaneal inversion.

In addition, it is possible that the potential dorsiflexion power of the embryonic tibialis anterior is much less than the adult condition because the marked inversion and adduction places the tendon close to the ankle joint axis. Furthermore, it is suggested that the tibialis anterior cannot exert significant dorsiflexion force until inversion and adduction of the forefoot are reduced. In contrast, the ability of the tibialis anterior to invert the subtalar joint is increased when the calcaneus is inverted (Jahss, 1982) as seen in the embryonic foot. Therefore, on the basis of tendon-axis relationships, it would appear that the embryonic tibialis anterior is a strong invertor of the forefoot, but a weak dorsiflexor of the ankle. This contrasts with its function in the adult limb where the tendon-axis relationships cause this muscle to be a strong ankle dorsiflexor but a relatively weak invertor of the subtalar joint, unless the calcaneus is inverted.

Distal Attachment of the Extrinsic Muscles

Whereas the distal attachment of the calcaneal tendon and the tendons of tibialis anterior and posterior seemed to replicate the adult condition, the results from this study suggested the distal attachment of the peroneal tendons and those terminating in the toes occurred relatively later than the other tendons. These distal attachments have not been previously documented with the exception of the single reference by Jones (1949) to the embryonic attachment of the peroneus longus tendon.

Peroneal Tendons: Of all the extrinsic muscles of the embryonic foot, the three peroneal muscles differed the most from their adult counterparts, the most striking contrast being peroneus tertius. Firstly, the tendon of peroneus tertius was not seen as a separate entity in any of the six embryos (see Fig 39C and 42). Although it is reportedly absent in about 10% of the adult population (Morton, 1942), this was not thought frequent enough to account for its apparent absence in all six embryos. Based on the reconstructions, it was concluded that the the tendon of peroneus tertius was still unseparated from that of extensor digitorum longus by the end of the embryonic period. It appeared to be represented by the most fibular fibers of the aponeurotic extensor digitorum longus which attached with the peroneus brevis to the base of the fifth metatarsal. These observations suggested that ontogenetically, peroneus tertius differentiates later than all the other muscular

elements in the embryonic foot.

At stage 20, none of the tendon fibers of peroneus tertius seemed to attach distally to the fifth metatarsal (as in the adult), but by stage 23 the unseparated tendon had attained a broad area of attachment to the base of the fifth metatarsal. Assuming that the forces exerted by this muscle would be related to the area of attachment of the fibers anchored distally, these observations suggest that the power and influence of peroneus tertius progressively increase during prenatal, and possibly postnatal, life.

Like peroneus tertius, peroneus brevis was seen to acquire increasing attachment to the base of the fifth metatarsal between stages 20 and 23 suggesting again, delayed distal attachment (see Fig 43). As in the adult foot, the distal fibers of the embryonic peroneus brevis appeared to blend with the distal fibers of the unseparated embryonic peroneus tertius in the vicinity of the base of the fifth metatarsal.

The tendon-and-sheath unit of the embryonic peroneus longus appeared to mature, coalesce or migrate from the fibular toward the tibial side of the sole of the foot, gaining attachments to the neighbouring bones along the way. These observations suggested that distal attachment of the peroneus longus was also delayed. Furthermore, by the end of the embryonic period, the tendon was attached distally only to the base of the first metatarsal; additional attachment to the first cuneiform, as in the adult foot, was not seen

in any of the embryos. This finding agrees with Jones (1949) who reported that peroneus longus does not attach to the first cuneiform until the fetal period.

Therefore, until stage 21, none of the three peroneal muscles were anchored distally at their definitive adult attachment site. On the basis of these observations, it would seem that until the later stages of embryonic development, the muscles acting to adduct and invert the forefoot (i.e. tibialis anterior and posterior) would be largely unopposed. It is conceivable that this might also be a factor contributing to the inverted and adducted posture of the embryonic forefoot.

The distal attachment of the embryonic peroneus longus was strikingly similar to that of lower groups of smaller sized primates described by Morton (1942). In both situations, the tendon attached to a long bony process on the first metatarsal (Fig 24). In the adult, no such process was observed or mentioned in the literature, and the distal attachment included both the first metatarsal and the first cuneiform bones. According to Morton (1942), the peroneus longus muscles of these lower primates is important for grasp, acting as an adductor of the first metatarsal; the bony prominence was thought to permit wide divergence of the hallux. Morton (1942) added that since the grasping function of the human (adult) foot has been long discarded and the hallux has become fixed in an adducted position, the tuberosity is correspondingly low and the insertion of

peroneus longus has been widened to gain attachment to the first cuneiform. These observations strongly suggest that the embryonic peroneus longus does not pronate the forefoot, as it does in the adult, but rather adducts the divergent hallux. In addition, it would appear that it cannot become an effective forefoot pronator until the hallucial divergence has been reduced and the distal attachment has been expanded to include the first cuneiform. These speculations are supported by Jones (1949) who reported that the reduction of forefoot inversion in the fetus coincides with the tendon of peroneus longus gaining its insertion on the first cuneiform, in addition to its first metatarsal attachment.

Long Extensor and Flexor Tendons: There were two striking features of the long extensor and flexor tendons in the embyronic foot. Firstly, the middle and distal phalanges, to which these tendons were destined to attach, were the last elements in the foot to chondrify. As indicated earlier, this raises questions related to the degree of attachment during the embryonic period and the consequent effect of these muscle. This is important because it is not until stage 23 that both the middle and distal phalanges were seen to be chondrified. Secondly, the long flexor and extensor tendons demonstrated an undulating course through the embryonic foot (Fig 35). Initially, this was interpreted as supportive evidence of the lack of distal attachment. However, the tendon of tibialis anterior

demonstrated similar undulations despite the fact that it was attached distally to both the first cuneiform and the base of the first metatarsal, as in the adult foot. Therefore, it was concluded that the tendinous undulations in the embryonic foot probably represented an artifact of histological preparation which was not directly related to the blastemal condition of the phalanges. No mention of this histological feature pertaining to the embryonic foot was found in the literature. The question of the strength of the distal attachment of these tendons could not be answered from the methodology employed.

Torsion of the Adult Tendons: To convert the embryonic posture of the foot to the anatomical position, the ankle must dorsiflex, the entire foot must evert and the forefoot must be abducted. It is proposed that eversion of the calcaneus, during prenatal and postnatal life, may cause the torsion of the calcaneal tendon that was observed in the adult limb. This proposal agrees with White (1943) who suggested that the torsion was caused by the changing relationships between the talus and calcaneus during prenatal development. Similarly, although again it cannot be proved in this study, it is proposed that pronation of the forefoot during ontogeny may account for the torsion of the tendon fibers of adult tibialis anterior. Torsion of the calcaneal tendon and the anterior tibial tendon was also described by Jones (1949) but he did not speculate on the cause.

The Intrinsic Muscles Attaching to the Calcaneus

As with the extrinsic muscles, the attachment of the embryonic intrinsic muscles often contrasted with those of the adult foot. Unfortunately, many of the findings from this study cannot be compared to the findings of other workers because previous documentation is very limited.

Abductor Digiti Minimi: Whereas all three muscles of the first layer of the sole attached proximally to the calcaneal tuberosity in the adult foot, during stages 20 through 23 only the muscle belly of abductor digiti minimi attached proximally to the calcaneal tuberosity (Figs 47 and 48). In three of the older specimens (embryos XXI, XXIIb and XXIII), the muscle made an intermediate attachment to the base of the fifth metatarsal before proceeding into the fifth toe. Similarly, the adult abductor digiti minimi demonstrated attachment to the base of the fifth metatarsal before terminating on the proximal phalanx of the fifth toe. Jones (1949) pointed out that (at least in the adult foot) a portion of abductor digiti minimi almost always attaches to the fifth metatarsal and that this part of the main muscle mass is known as abductor ossis metatarsi digiti quinti. Although the significance is uncertain, it is interesting to note that in the embryonic foot, the distal attachment site (i.e. the base of the fifth metatarsal) of this muscle was chondrified earlier than the proximal phalanges to which abductor digiti minimi proper, as well as flexor digitorum brevis and abductor hallucis, will eventually attach. If, as

suggested earlier, a chondrified skeletal element provides a more secure attachment than a mesenchymal element, then it is possible that abductor ossis metatarsi digiti quinti would be able to exert more effective forces on the embryonic foot sooner than the other muscles of the first layer.

Abductor Hallucis: In contrast to the abductor digiti minimi and the abductor ossis metatarsi digiti quinti, the muscle bellies of flexor digitorum brevis and abductor hallucis did not extend as far proximally as the calcaneal tuberosity. The muscle belly of abductor hallucis was well defined in the midfoot of all the embryos; distally it fused with the tibial head of flexor hallucis brevis, as in the adult foot. However, more proximally it faded in the region of the sustentaculum tali, appearing to blend with the radiating fibers of tibialis posterior (see Figs 36A and 48B). In contrast, no adhesion between the adult abductor hallucis and the tibialis posterior was detected in the dissected adult limb; proximal attachment was restricted to the tibial side of the calcaneal tuberosity (Fig 48A).

Documentation of adhesions between the abductor hallucis and the tibial posterior was found in only one source which pertained to the postnatal foot. Turco (1981) reported that in some cases of congenital club foot associated with severe cavus deformity, abductor hallucis may be abnormally attached to the tendon sheath of tibialis posterior and the two flexor tendons as well as the

navicular tuberosity.

Flexor Digitorum Brevis: As previously indicated, the muscle belly of the embryonic flexor digitorum brevis did not attach to the calcaneal tuberosity as the adult limb showed (Figs 48 and 49). However, between stages 20 and 23, the muscle appeared to have grown in length towards the calcaneal tuberosity. The transparency model of embryo XXIIa demonstrated a backwards projecting band of tissue which appeared to attach to the calcaneal tuberosity (Fig 48B). Similarly, the sagittal sections of embryo XXIIb showed the continuity between the proximal portion of the fleshy muscle belly and a thin mesenchymal condensation which attached with the plantar aponeurosis to the calcaneal tuberosity (Fig 50). In the adult foot, the muscle was similarly adhered to the plantar aponeurosis, but the fleshy part of the belly extended proximally to the calcaneal tuberosity. These observations seemed to indicate that the muscle matures in a distoproximal sequence, demonstrating an adherence to the plantar aponeurosis near the calcaneal tuberosity by at least stage 22.

Quadratus Plantae: In contrast to the embryonic flexor digitorum brevis, proximal attachment of the quadratus plantae to the calcaneus was apparent throughout the embryonic series. This differs from Cihak (1972) who claimed that this attachment is not formed until after 30mm CRL. This discrepancy is possibly attributable to different methods of aging.

As in the adult, the embryonic quadratus plantae attached distally to the tendons of flexor hallucis longus at all stages (Fig 33C and D). The only obvious difference between the embryonic and adult conditions was that up to stage 22, the muscle existed as a single mass that had not yet differentiated into two distinct heads. The functional significance of this late differentiation was not apparent.

Extensor Digitorum Brevis: In the dorsum of the foot, the extensor digitorum brevis was well-defined throughout the series, with proximal attachment to the calcaneal sulcus and the cervical ligament as seen in the adult (Fig 45). However, unlike the adult foot, where this attachment site was largely obscured by the overlying talus (Fig 46), the embryonic site of attachment was very exposed. This was attributed to the inverted position of the calcaneus, causing the calcaneal sulcus to be directed outward. Similarly, Bohm (1929) reported that the dorsal surface of the embryonic calcaneus was tilted laterally (i.e. outward).

Influence of the Intrinsic Muscles: This study could not investigate the actual function of the muscles described. However, there are clear differences when compared to the adult, particularly with respect to muscle attachments, bone relationships, muscle maturity and joint axes which all directly contribute to the effects of muscle contraction and function. It might therefore be profitable to suggest ways in which the intrinsic muscles could

influence the development of the foot, focusing in particular on the orientation of the calcaneus.

It is postulated that the three muscles of the first layer of the sole might function in a manner similar to guy wires to neutralize the position of the calcaneal tuberosity in relation to the forefoot. The delayed proximal attachment of the flexor digitorum brevis and abductor hallucis seem to create an imbalance of power in the embryonic foot which might permit the abductor ossis metatarsi digiti quinti and the abductor digiti minimi to pull the calcaneal tuberosity in a fibular direction. In effect, this could medially rotate the calcaneus along its long axis, thereby everting it. Since contraction of abductor hallucis, might invert the calcaneus through forces exerted on the calcaneal tuberosity, delayed attachment of this muscle may permit the fibular-sided muscles to help reduce the calcaneal inversion without opposition.

Based on the sequence of chondrification, the attachment of abductor ossis metatarsi digiti quinti to the base of the fifth metatarsal might ensure that this muscle is anchored more effectively both distally and proximally in advance of all other muscles in the first layer. Assuming that proximal and distal anchoring of a muscle is a prerequisite for exerting forces on the skeletal elements, it would seem reasonable to conclude that the abductor ossis metatarsi digiti quinti would be able to exert its influence before the other muscles of the first layer. Clearly, the

muscle bellies of flexor digitorum brevis and abductor hallucis were not attached to the calcaneal tuberosity by the end of the embryonic period (stage 23). Therefore, the forces exerted by these muscles on the embryonic calcaneus would seem to be restricted.

Therefore, on the basis of the numerous differences between the embryonic and adult musculature, it was concluded that muscular function in the embryonic foot would differ greatly from the adult condition. Furthermore, it was thought that these differences might account in part for the contrasting postures of the embryonic and adult foot. Although it was not possible to identify the mechanisms controlling the postural changes during ontogeny, the findings from this study pointed to both differential growth of the skeletal elements as well as changing muscle function as two possible factors.

Comparison of the Embryonic Foot to Congenital Foot Anomalies

When the features of the embryonic foot were compared with the pathoanatomy associated with various congenital foot anomalies, several similarities were identified. The most striking resemblance was between the embryonic foot and talipes equinovarus.

Talipes Equinovarus (Congenital Clubfoot): As indicated previously, the postural features of the embryonic foot included plantar flexion (equinus) at the ankle joint and calcaneal inversion (varus) at the subtalar joint along with forefoot adduction and inversion (varus). These same features are the hallmarks of congenital clubfoot (Hauser, 1966; Lehman, 1980; Salter, 1981; Turco, 1981) (Fig 54). Two features of the embryonic lower limb not seen in clubfoot were the marked lateral rotation of the limb as a whole and the absence of a tibial longitudinal arch. Despite these differences, the striking similarity between the embryonic foot and the congenital clubfoot strongly suggested that in clubfoot, the key embryonic postures have persisted. This agrees with Bohm (1929), Scherb (1931), Martinez-Cuadrado and Gonzalez-Santander (1967) and Victoria-Diaz and Victoria-Diaz (1984). However, it disagrees with Bessel-Hagan (1889, cited in Bohm, 1929) and his supporters who insisted that at no time does the embryonic foot resemble the clubfoot.

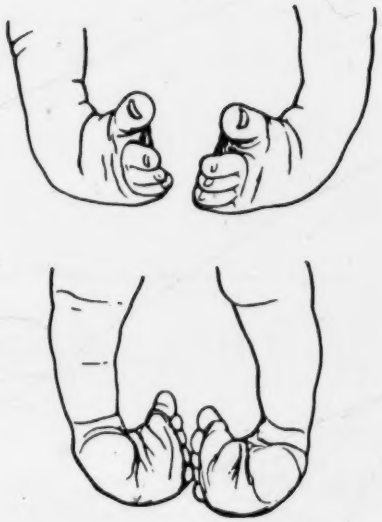


Fig 54 Talipes equino-varus (congenital clubfoot).

In addition to the postural similarities, several skeletal features of the embryonic foot, which were described earlier, have been observed in some cases of clubfoot:

1. inward rotation of the posterior 1/3 of the calcaneus (Schlicht, 1963)
2. a proportionately short calcaneus (Irani and Sherman, 1963; Schlicht, 1963)
3. a proportionately short first metatarsal (Schlicht, 1963; Wynne-Davies, 1964b; Lehman, 1980; Turco, 1981)
4. absence of the usual constriction of the talar neck (Irani and Sherman, 1963; Huurman, 1978; Turco, 1981)

From the reconstructions of the horizontally-sectioned embryos XXIIa and XXIII, the angle between the long axes of the talus and calcaneus was determined (see Fig 9J). This anteroposterior (AP) talocalcaneal angle measured 20° in embryo XXIIa and 11° in embryo XXIII (Table 3). According to Huurman (1978), this angle is typically between 20 and 40 ° in the postnatal foot, but in clubfoot this angle is reduced sometimes to 0°. The fact that less than normal values for the AP talocalcaneal angle are seen in clubfoot and in embryo XXIII, points to yet another characteristic of clubfoot that seems to represent a persistent late embryonic feature. It should also be noted that unlike the younger specimens, embryo XXIII demonstrated marked adduction of the forefoot, which is one of the characteristic features of clubfoot. Therefore, of all the embryos studied, the

skeletal arrangements found in embryo XXIII bore the greatest resemblance to clubfoot.

Pathology of the muscles is commonly reported in clubfoot. For example, some workers have observed that in clubfoot, the typical medial expansion of the calcaneal tendon at its distal attachment is more accentuated, thereby perpetuating the varus heel deformity (Stewart, 1951; Schlicht, 1963; Ippolito and Ponsetti, 1980). Similarly, it was observed from the reconstruction of embryo XXI, that the calcaneal tendon appeared to attach higher on the tibial side of the calcaneal tuberosity (Fig 32). On the basis of this similarity, it is possible that malinsertion of the calcaneal tendon, as reported in some cases of clubfoot, has its origin in the embryonic period. However, other investigators have reported that the distal attachment of this tendon in clubfoot does not differ from the normal foot (Irani and Sherman, 1963; Waisbrod, 1973). Lehman (1980) suggested instead that the calcaneal tendon only appears to be malinserted due to the inverted position of the calcaneus.

Anomalous attachments of the peroneus longus tendon to the lateral metatarsals were observed by Stewart (1951) in some cases of clubfoot and he speculated that these aberrant attachments prevent the peroneus longus from exerting its pronatory forces on the forefoot. In light of these observations, it was interesting to note that in the embryonic foot, the tendon-and-sheath unit of peroneus

longus also demonstrated adherence to the lateral metatarsals (Fig 42). This similarity suggested that the aberrant attachments of peroneus longus, sometimes seen in clubfoot, might represent the persistence of yet another embryonic characteristic.

As previously mentioned, Turco (1981) reported that in some cases of clubfoot associated with a severe cavus deformity, abductor hallucis is abnormally adhered to the tendon of tibialis posterior. He considered this abnormal adherence to be a postnatal adaptive change. However, the observation of a similar adherence in the embryonic feet (Fig 48B) suggested that in clubfoot, this feature may represent instead the persistence of an embryonic characteristic.

In summary, the findings from this study strongly suggest that the postural features of clubfoot, as well as certain aspects of its pathoanatomy, represent persistent embryonic characteristics. Therefore, in general terms these findings do agree with the reports by Bohm (1929), Scherb (1931), Martinez-Cuadrado and Gonzalez-Santander (1967) and Victoria-Diaz and Victoria-Diaz (1984) that the theory of arrested development is a likely cause of congenital clubfoot. However, the term "arrested" may be misleading for it implies a complete absence of further development, including growth, beyond the embryonic period. Perhaps, it would be more accurate to simply state that congenital clubfoot occurs when certain the embryonic characteristics

of the foot are retained. This study has not attempted to identify the factors that account for the persistence of these embryonic features.

Whereas clubfoot seems to replicate the postural features of the late embryonic foot (i.e. stage 23), other less severe congenital anomalies of the foot seem to arise when only one or two of the embryonic characteristics have been retained. These anomalies are described below.

Metatarsus Adductus/Varus (Fig 55A): As previously mentioned, embryo XXIII, demonstrated marked adduction of the forefoot, a feature that is also characteristic of clubfoot. Forefoot adduction is also seen as an isolated postural anomaly without hindfoot involvement. In this situation, it is referred to as metatarsus adductus/varus (Wynne-Davies, 1964b).

Forefoot Varus (Fig 55B): The congenital anomaly described as forefoot varus presents with only inversion of the forefoot. Kolker (1973) attributed it to a lack of ontogeny. According to Jahss (1982), the talar neck exhibits less torsion than normal in this condition. Similarly, forefoot inversion and a lack of talar neck torsion were found to be characteristic of the embryonic foot.

Congenital Equinus (Fig 55C): Equinus is as postural deformity in which the heel is elevated and the ankle is plantar flexed (Cailliet, 1983). According to Kolker (1973) congenital equinus is associated with a congenitally short

Fig 55 Less severe congenital foot anomalies apparently representing persistant embryonic characteristics.

A) Metatarsus adductus/varus.

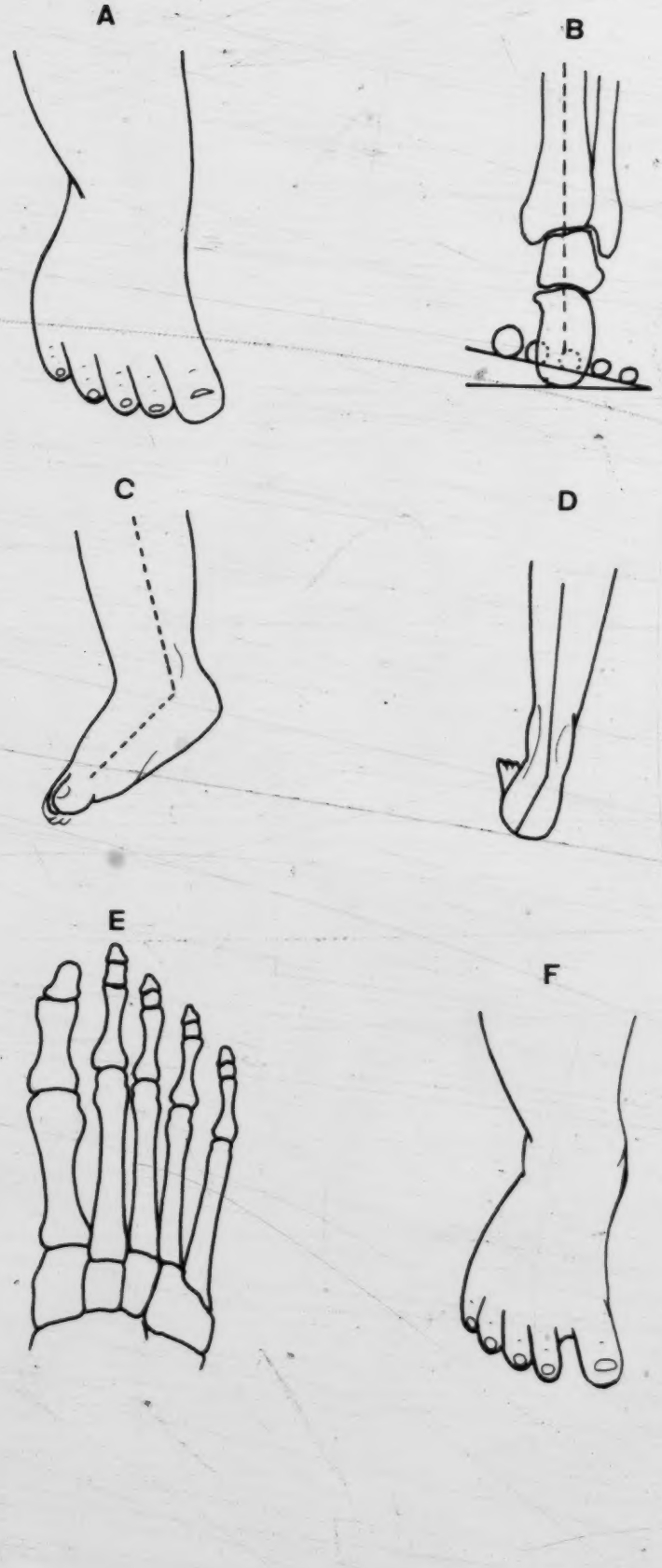
B) Forefoot varus.

C) Congenital equinus.

D) Calcaneal varus.

E) Short first toe.

F) Metatarsus primus varus.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gastrocnemius or triceps surae as a whole. Since plantar flexion of the ankle is also seen in the embryonic foot, equinus appears to be a persistent characteristic of the embryonic period. This conclusion is supported by Robbins (1982) who similarly reported that equinus is caused by the "abnormal persistence of a fetal state".

Calcaneal Varus (Fig 55D): As indicated earlier, inversion of the calcaneus is a well-recognized feature of the embryonic foot. In the congenital postural deformity referred to as calcaneal varus, the distinguishing feature is also inversion of the calcaneus. Kolker (1973) attributed this condition to a lack of ontogeny whereby insufficient pronation of the calcaneus has occurred.

Short First Toe (Fig 55E): Morton (1942) was the first to draw attention to the congenitally short first toe, thereafter called "Morton's Toe". As in the embryonic foot, the congenitally short hallux is attributed to a proportionately short first metatarsal, and appears to represent the persistence of another isolated embryonic feature.

Metatarsus Primus Varus (Fig 55F): The congenital foot anomaly of metatarsus primus varus, presents with a divergent hallux due to the wide angle between the first and second metatarsals. This anomaly is strikingly similar to the hallucial divergence seen in the embryonic foot, strongly suggesting that it represents the persistence of an isolated embryonic characteristic.

VI. SUMMARY

The present study examined the postures and musculoskeletal structures of the human foot during the last four stages of embryonic development (i.e. stages 20 to 23). In contrast to much of the previous literature, the skeletal relationships in the embryonic hindfoot were found to be similar to the adult condition:

1. the calcaneus was situated below the talus
2. the fibula projected further distally than the tibia
3. there was no evidence that the tip of the fibular malleolus was in contact with the calcaneus

The postural features during stages 20 through 23 included:

1. lateral rotation of the limb as a whole
2. extreme plantar flexion at the ankle
3. adduction of the foot toward the tibia
4. calcaneal inversion
5. forefoot inversion
6. absence of the tibial longitudinal arch
7. hallucial divergence at stage 22
8. marked forefoot adduction at stage 23

It was thought that the axes of rotation of the ankle and subtalar joints as well as tendon-axis relationships might account in part for the combination of ankle plantar flexion, calcaneal inversion and adduction of the foot which was characteristic of stages 20 through 23. The contrasting postures of the embryonic and adult foot were also attributed in part to numerous striking differences in their

respective musculature. In particular, the relatively later distal attachment of the embryonic peroneal tendons as well as the tendons terminating in the toes, concommitant with the late proximal attachment of the abductor hallucis and flexor digitorum brevis were identified. Although it was not possible to identify the factors that would convert the embryonic foot posture to the adult anatomical posture, the findings from this study pointed to both differential growth of the skeletal elements as well as changing muscle function as two possible factors.

Numerous similarities between the embryonic foot and congenital clubfoot were identified. Some of these common points have been documented by other workers. Other similarities, pertaining to the muscles and tendons, have not been previously observed. Therefore, this study supports and extends the contention that clubfoot seems to be characterized by arrested development, or more accurately, the persistence of certain embryonic features. In addition, subtle congenital variations seem to occur when only one or two of the embryonic characteristics have been retained in an otherwise "normal" foot.

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VIII. APPENDICES

A. APPENDIX A: METHOD OF WAX-PLATE RECONSTRUCTION USED FOR EMBRYO XXIIa

Adapted from Born's (1887) method as described by Bardeen (1901)

Materials

1. 1.36mm thick plates (15 x 24mm) of pink dental modelling wax (Kerr Flexo Wax)
2. white glue
3. straight pins to facilitate alignment of wax-plates
4. 16 gauge wire for reinforcing
5. white paper for tracing
6. cellophane tape

Equipment and Tools

1. Bausch and Lomb microprojector, catologue number 42-63-59
2. pencil
3. micrometer slide
4. metric ruler
5. pencil for tracing
6. Picker X-ray light box, model number 240091
7. scratch awl
8. modified C920 microdissecting scalpel
9. artist' brush (approximately .5mm wide)
10. Bunsen burner
11. small, metal spatula

Procedure

1. The required magnification for the reconstruction was determined to be 34X by dividing the thickness of the wax plates (1.36mm) by the thickness of the serial sections (40 μm).

2. The microprojector was set up to project downwards onto a horizontal drawing surface.

3. To obtain the correct magnification of the projected image, the micrometer slide was projected onto the drawing surface. Various combinations of objective power and distance between the projector and the working surface were tried until the 1mm scale of projected micrometer image measured 34mm with the metric ruler.

4. Each serial section was projected in turn onto white paper which was secured to the drawing surface.

5. Using the pencil, the outlines of the external form of the foot and the definitive cartilage elements were

traced onto the paper. The phalanges and the condensed mesenchyme (perichondrium) which enclosed each of the elements was omitted. One tracing was produced for each of the serial sections of the foot (Fig 56A).

6. Using the transillumination provided by the light box, the serial tracings were superimposed and aligned relative to each other using the method of best fit. The tracings were secured together along one edge with cellophane tape. To retain the established alignment during the remainder of the procedure, four points of reference were drawn on the lowermost tracing. These points were then copied onto each of the overlying tracings.

7. The uppermost sheet of paper was separated from the pile of tracings, secured to the light box and a plate of wax was placed on top. With the aid of transillumination, the contours could be viewed through the translucent wax and using the scratch awl, the outlines of the skeletal elements and the three references were etched onto the surface of the wax.

8. The scalpel was used to cut through the wax along the etched contours, ensuring that bridges of wax connected all of the individual profiles to produce a single unit (Fig 56B).

9. To remove the lip of wax along the edges of the cut contours, both surfaces of the wax plate were planed with a razor blade held at about 80 degrees to the horizontal.

10. The single unit of contours was carefully separated from the background.

11. One straight pin was pushed upwards through each of the three reference points.

12. The next tracing was separated from the pile and reproduced in the same manner on another plate of wax.

13. White glue was brushed onto the upper surface of the first cut wax-plate. The second plate was realigned with the first by pushing the reference pins up through the appropriate reference points. The two plates were gently pressed together and the excess glue was wiped off.

14. These steps were repeated until all of the tracings had been cut from the wax plates and the all the plates had been adhered together. This process involved the inclusion of wire bridges to take the place of the temporary wax bridges.

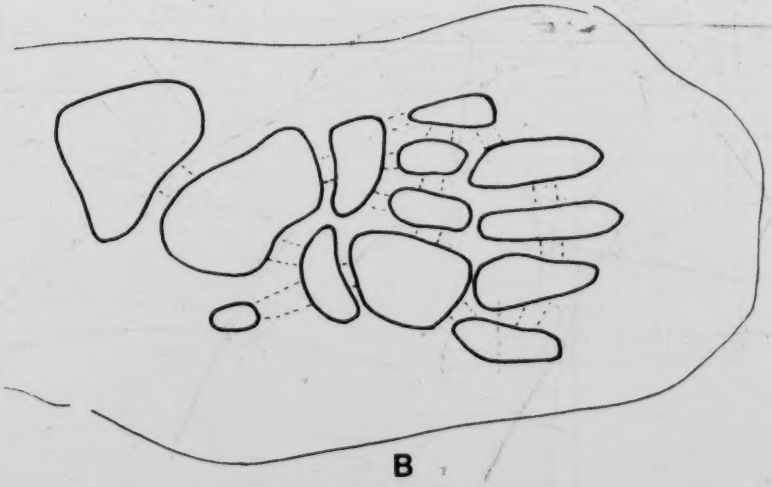
Fig 56. Production of wax-plate reconstruction.

A) Horizontal section from embryo XXIIa.

B) Tracing of the external form and definitive cartilage elements (solid line) from A) with temporary wax bridges (broken lines).

C) Completed wax-plate reconstruction of embryo XXIIa (dorsal view).

A



B

C

15. The metal spatula was heated over the flame of the Bunsen burner and used to remove the wax bridges and smooth the stepped edges to create a flowing outline. Short lengths of wire were also heated over the burner and inserted into the model at the weak points. The model was now complete (Fig 56C). Finally, the model was photographed from various angles.

B. APPENDIX B: METHOD OF TRANSPARENT RECONSTRUCTION USED FOR EMBRYOS XXa, XXI, XXIIa and XXIII

The specifications for each of the four reconstructions is contained in table 4.

Materials

1. 5 mil (.125mm thick) sheets of transparent acetate, 50 cm x 125 cm
2. 8 ply (.75mm thick) white bristol board, 55 cm x 70 cm (for reconstruction of embryos XXa and XXIIa)
3. 6mm thick white foamcore (for reconstruction of embryos XXI and XXIII)
4. glue sticks (FaberCastell UHU stic)
5. methyl alcohol (to erase ink contours from acetate)
6. masking tape

Equipment and Tools

1. Bausch and Lomb microprojector, catologue number 42-63-59
2. permanent (alcohol soluble) markers for overhead tranparencies - one each of black, green, red, purple, brown, blue, orange (Stabilo Lumocolour, fine and superfine)
3. Picker X-ray light box, model number 240096
4. paper cutter (64mm x 64mm)
5. utility knife

Procedure

1. Based on the thickness of the proposed spacers and the distance between the sections that were traced, a suitable magnification for all four of the reconstructions was determined to be 82X.

2. The microprojector was set up to project onto the back of an inclined work surface by adapting Sack's (1966) method of back-lit projection (Fig 57)

3. To obtain the correct magnification of the projected image, the micrometer slide was projected onto the drawing surface. Various combinations of different objectives and varying distances between the projector and the drawing surface were tried until the 1mm scale of the projected micrometer image measured 82mm with the metric ruler. The inclination of the head of the projector, the tilt of its mirror and the angle of the work surface were manipulated until the projected image was free from distortion in both the horizontal and verticle planes.

4. The full-size sheets of acetate were cut into smaller size rectangles, large enough to accomodate one tracing from each of the serial sections.

TABLE 4. SPECIFICATIONS PERTAINING TO CALCULATION OF THICKNESS OF FRAMES TO SEPARATE TRACINGS IN THE TRANSPARENT MODELS ENLARGED 82X

Embryo #	Section Thickness (um)	Sequence of Sections Used in Transparent Models	Distance Between Traced Sections (um)	Frame Material and Thickness	Number of Framed Tracings
XXa	20	every section	20	double-thick bristol board 1.5 mm	70
XXI	10	every 8th section	80	foamcore 6.0 mm	20
XXIIa	40	every section	40	quadrupel-thick bristol board 3.0 mm	31
XXIII	20	every 4th section (est)	80	foamcore 6.0 mm	20

Fig 57.Set up for back lit projection.

The microprojector (M) projects the image of the serial section onto the back of an inclined drawing surface (DS) which consists of a thick plate of glass, the upper surface of which is covered with tracing paper. The image shines through the glass and is formed on the underside of the tracing paper. The translucent nature of the tracing paper permits the image to be viewed through the paper. This set up permits the contours to be traced from the projected image.

5. For each section to be traced, one smaller size sheet of acetate was temporarily secured to the tracing paper with masking tape. Using the coloured pens, the external form of the foot and the internal structures were traced from the projected image: definitive cartilage elements (black); mesenchymal elements, such as precartilage, perichondrium, interzones and developing ligaments (green); nerves (purple); blood vessels (red); muscles (blue); tendons (brown); plantar aponeurosis (orange) (see Fig 58).

6. With the aid of transillumination, the acetate tracings were superimposed in sequence and aligned with each other using the best fit method. Since the tracings contained numerous contours representing a large number of structures, the relative orientation of each tracing was fairly easy to determine. Once this orientation had been established, the newly aligned acetate tracing was temporarily secured to the underlying sheet with masking tape. When all of the tracings had been brought into register, four reference points were marked on the sheet at the bottom of the pile. These points were copied onto each of the overlying sheets so that the established alignment would be retained throughout the remainder of the procedure.

7. Each tracing was subsequently mounted on a frame to separate the acetate sheets by a distance that would recreate the third dimension to its correct proportion. The thickness of the frame was determined by the distance between the sections that were traced and the magnification. To construct these frames, 3.75 cm wide strips were cut from sheets of either bristol board or foamcore, using the paper cutter or the utility knife respectively. One strip was glued to each of the four edges of the acetate sheet to form the frame. The framing procedure utilized a template specially designed for each of the reconstructions to prevent sagging of the acetate sheets, preserve the established alignment and ensure consistent outside dimensions of the frame which now served as alignment references.

8. Finally, the mounted tracings were stacked in sequence and the contours were brought into register by lining up the outer borders of the frames. The individual mounted tracings were not adhered together. As a result, it was possible to examine: individual tracings; a short series of tracings from above or below, in front or behind, the tibial or fibular side, depending on the plane of section (Fig 59) and compare tracing(s) from one region (e.g. hindfoot) with tracing(s) from another region (e.g. forefoot).

Fig 58.
A) Horizontal section from embryo XXIIa.
B) Tracing of external form and internal structures from section in A).
black: outline of limb and definitive cartilage;
green: condensed mesenchyme, perichondrium, ligaments;
blue: muscle;
brown: tendon;
purple: nerve;
red: blood vessel

Fig 59. Completed transparency reconstruction of embryo XXIIa.

A) The entire model containing 31 mounted acetate tracings, viewed from above by transillumination.

B) A short series containing 16 tracings viewed from below.

C. APPENDIX C: DEVELOPMENT OF THE METHOD OF TRANSPARENCY RECONSTRUCTION

The method for the transparency reconstruction was adapted from Gaunt and Gaunt (1978), through a process of trial and error. The objectives were to devise a technique that would:

- minimize the number of times the tracings were reproduced to enhance the time efficiency and reduce error
- maximize the overall transparency of the reconstruction to facilitate the visualization of the internal structures

Various "transparent" materials were tried as well as different methods of producing the contours:

Photocopying the microphotographs: Each serial section was photographed and the enlarged black and white photomicrographs were photocopied onto standard photocopy tranparencies. This technique proved to be unsuitable because the limited transparency of the photocopied image would not allow visualization through more than about five superimosed transparencies.

In an attempt to enhance the transparency of each image, the photomicrographs were printed directly onto panatomic X film, following the example of Brown and Arnott (1971) who used orthochromatic lithofilm. Unfortunately, this method was no better than the forementioned due to the limited transparency of the image on the film.

Tracing the Contours from the Micrographs: Abandoning the photographic reproduction of the serial sections, the outlines of the internal structures were traced from the enlarged microphotographs onto photocopy transparency film. This proved unsatisfactory because it was difficult to discern all the outlines from the microphotograph. Furthermore, it was not possible to view through more than about ten superimposed tracings because of the slightly cloudy nature of the transparency sheets.

Tracing the Contours from the Image Produced by Back-Lit Projection onto Acetate Sheet: The most suitable material proved to be 5 mil acetate sheet, although not perfectly transparent due to its slight bluish tinge. About 30 superimposed tracings could be viewed through at one time. This material had the added benefit of coming in 20 X 50 inch (510mm X 1275mm) sheets which could be cut to the desired size. In contrast, transparency sheet came no larger than 8.5 X 14 inches (216mm X 355mm). A method of back-lit projection, adapted from Sack (1966) was used to produce an enlarged image of each serial section.

Another variable in the construction of transparency models was the spacers which separated the serial tracings to establish the correct perspective of depth (see Table 4).

Various materials and thicknesses were tried:

Acetate Sheet Spacers: Acetate sheets between the serial tracings proved unsuitable because the cumulative effect of the bluish tinge greatly limited light transmission.

Plexiglas Plate Spacers: Plexiglas plates, though individually more transparent than acetate, also limited light transmission when several plates were stacked together. In addition, this material was comparatively expensive, more difficult to cut to exact dimensions and the completed model was very heavy and unwieldy.

1.5mm Bristol Board Frames: To prevent any further limitation of light transmission, each acetate sheet was mounted instead on an individual frame of bristol board, which separated each consecutive tracing by 1.5mm. This method was used for embryo XXa; each of the 20 µm sections was traced and the completed model was comprised of 70 acetate tracings. Unfortunately, it was not possible to view through all the tracings at once, necessitating that the model be studied in segments.

3mm Bristol Board Frames: For embryo XXIIa, 3mm bristol board frames were used to separate each of the 40 µm sections which were traced. The model totalled 31 sections and could be viewed in its entirity.

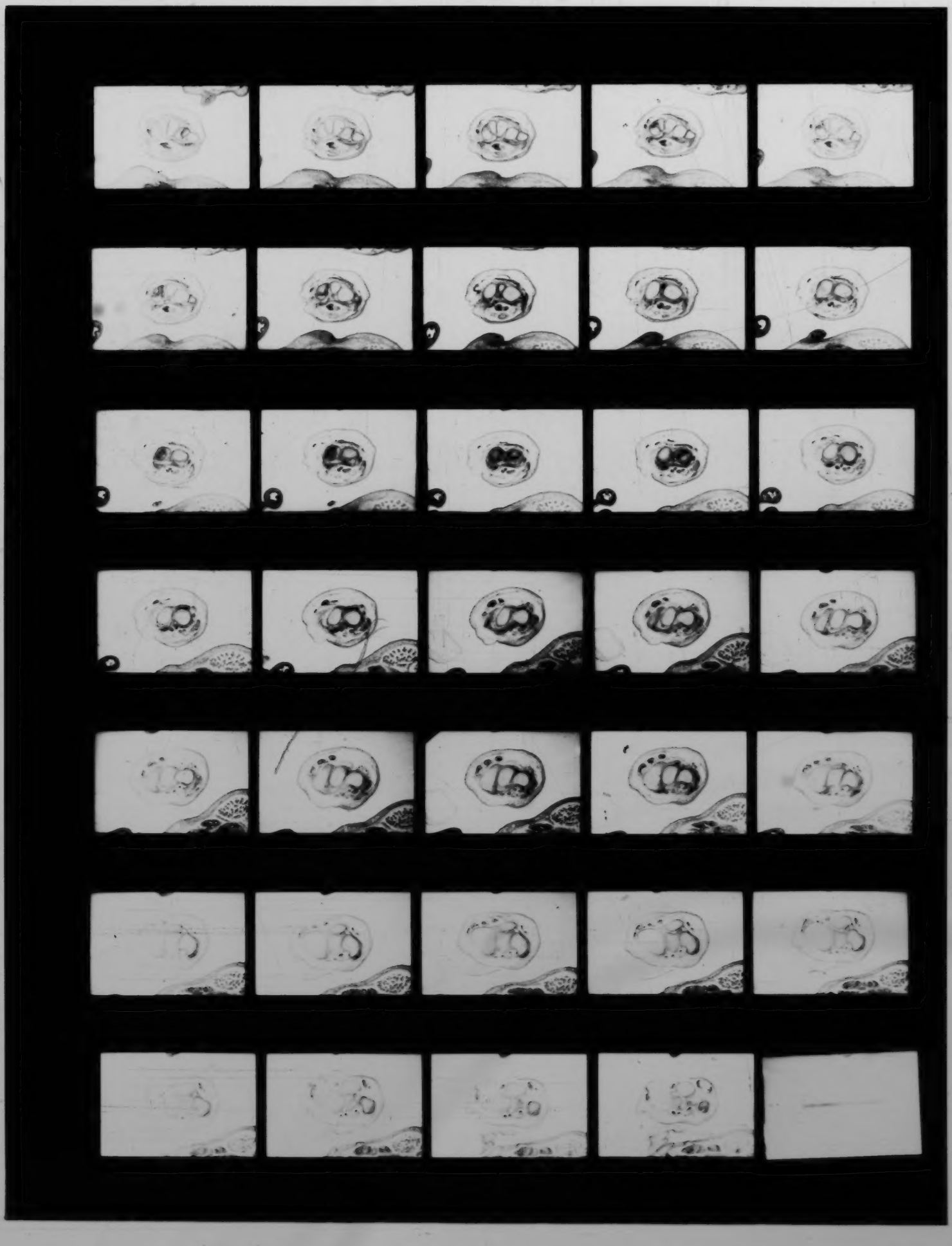
6mm Foamcore Frames: For embryos XXI and XXIII, 6mm thick foamcore frames were used. In embryo XXI, one in eight of the 10 µm sections were traced, whereas in embryo XXIII, one in four of the 20 µm sections were represented. Each of the completed models was comprised of 20 mounted tracings. The foamcore proved to be more suitable than bristol board because it was less flexible and much lighter. Also, it was not necessary to laminate several layers together as with the bristol board, to get the 6mm thickness. The models with foamcore frames were therefore easier to construct, handle and more durable.

D. APPENDIX D: PHOTOMICROGRAPHS OF SERIAL SECTIONS OF EMBRYOS XXa, XXB, XXI, XXIIa, XXIIb and XXIII

EMBRYO XXa: Sagittal sections through the right leg and foot, viewed from the fibular side, progressing from the tibial to the fibular side of the limb.

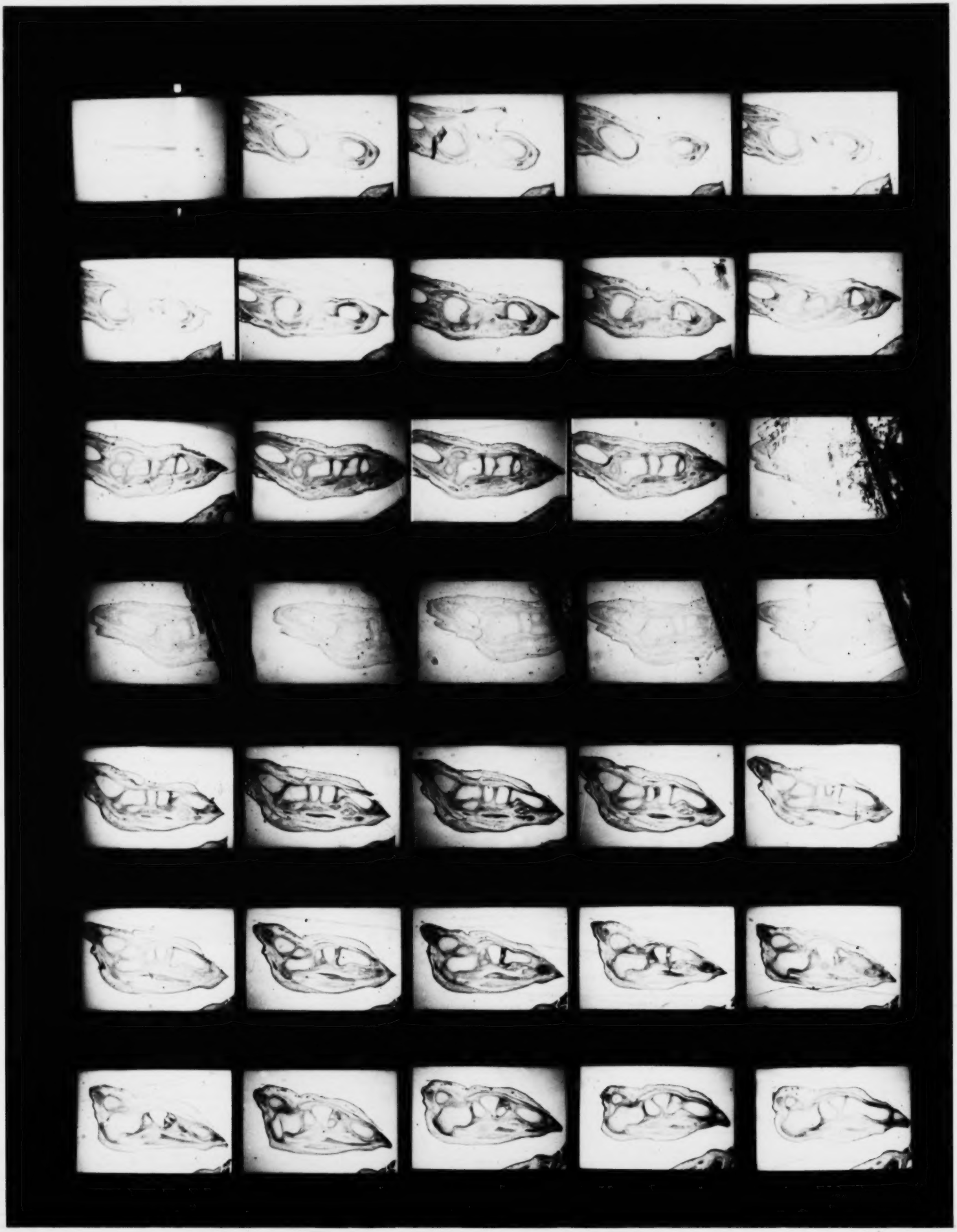
EMBRYO XXb: Coronal sections through the right foot, viewed from behind, beginning with the midfoot and progressing proximally to the hindfoot.

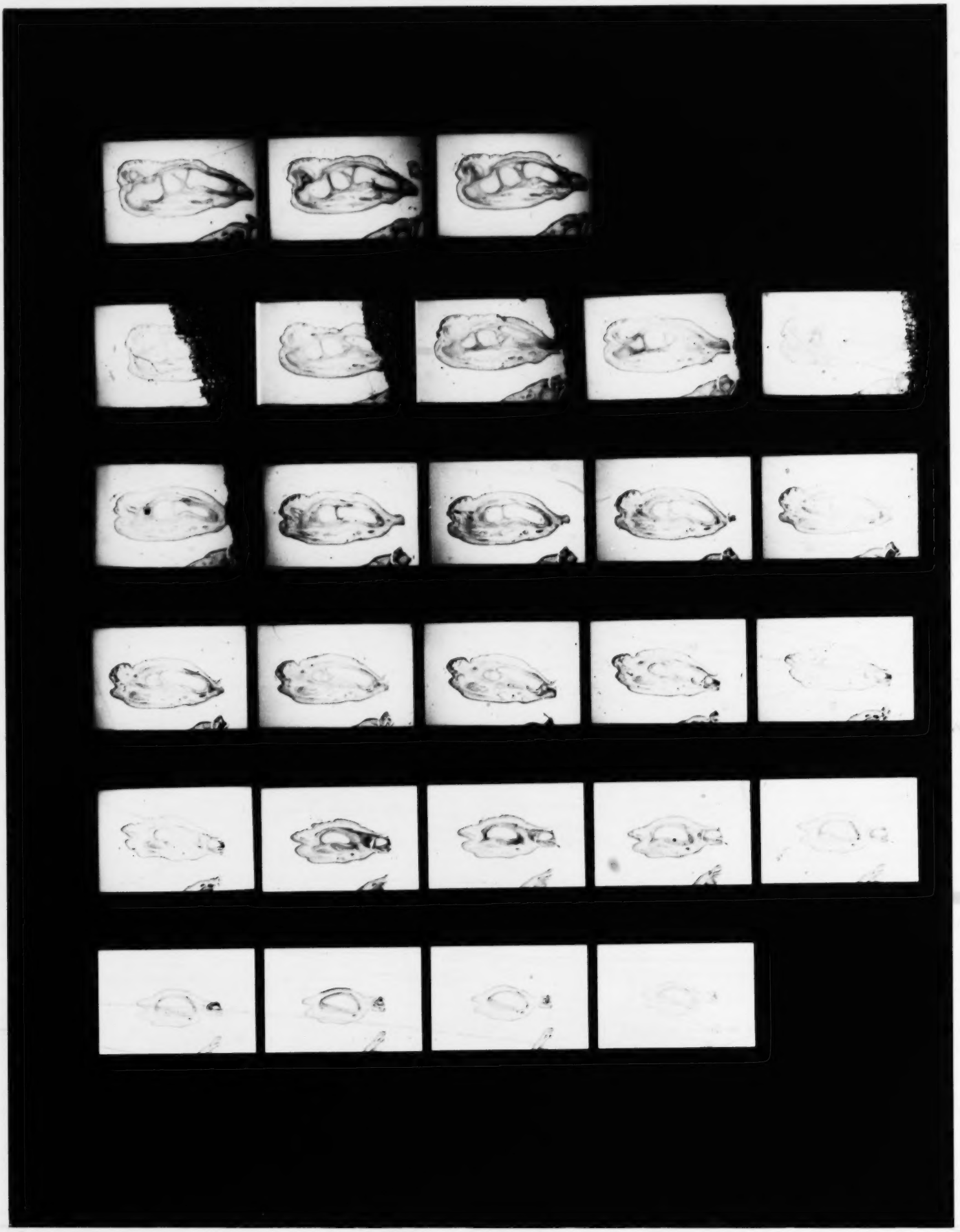
EMBRYO XXI: Coronal sections through the right foot, viewed from behind, beginning with the midfoot and progressing proximally to the hindfoot.



EMBRYO XXIIa: Horizontal sections through the right foot viewed from above, progressing from the dorsal to the plantar aspect of the foot.

EMBRYO XXIIb: Sagittal sections through the right leg and foot, viewed from the fibular side, progressing from the tibial to the fibular side of the limb. (two pages)





EMBRYO XXIII: Horizontal sections through the left foot, viewed from above, progressing from the dorsal to the plantar aspect of the foot.